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## TRANSACTIONS

OF THE

# AMERICAN PHILOSOPHICAL SOCIETY,

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FOR PROMOTING USEFUL KNOWLEDGE.

VOLUME XX.-NEW SERIES.

PART I.

ARTICLE I.—The History of the Pelycosauria, with a Description of the Genus Dimetrodon, Cope. By
G. Baur and E. C. Case.

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## TRANSACTIONS

OF THE

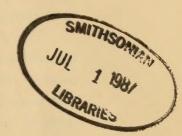
## AMERICAN PHILOSOPHICAL SOCIETY.

#### ARTICLE I.

THE HISTORY OF THE PELYCOSAURIA, WITH A DESCRIPTION OF THE GENUS DIMETRODON, COPE.\*

BY G. BAUR AND E. C. CASE.

Read before the American Philosophical Society, March 3, 1899.



#### HISTORICAL.

The first remains of Permian Reptiles in the United States were described by Prof. Cope¹ in 1875 from near Danville, Vermillion county, in eastern Illinois. It was left undecided whether the strata from which the fossils came belonged to the Triassic or the Permian. The vertebrate remains are unaccompanied by invertebrate fossils, but the invertebrate remains of the region are all Carboniferous forms. Mr. Gurley, of Danville, the discoverer of the fossils, considers that the vertebrate remains came from deposits in the bed of an ancient river of the Permian time which cut through the underlying Carboniferous rocks. This, if true, explains the puzzling feature of these typically Permian forms occurring on the same level with the Carboniferous invertebrates.

The genus and species *Clepsydrops collettii* Cope was established, based on cervicals, including the axis, dorsal and caudal vertebræ; besides proximal ends of ribs, an

\*PREFATORY NOTE.—The unfortunate death of Dr. Baur left the manuscript of this article in the hands of the junior author in an unfinished condition, and he has attempted to complete it with as little change from the original portion written by Dr. Baur as possible. The historical part, with the exception of the Russian and the Bohemian forms, and a portion of the African forms, was the work of Dr. Baur. The description of the skeleton was the work of the junior author, with the advice of Dr. Baur.

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astragalus, considered first as a coracoid bone, and some phalanges, which were provisionally referred to the same genus. The vertebræ are deeply biconcave, and notochordal. There are no processes on the centra, but a small capitular, articular face is present on the anterior articular edge of two of the dorsals. The dorsal vertebræ have the sides somewhat contracted; in one specimen the inferior face rounded, in another it is longitudinally acute. The diapophysis does not project far beyond the base of the neural arch, and is compressed. The caudals are elongate. Then follow remarks about the ribs, astragalus and phalanges. That these remains belonged to a small animal is indicated by the size of the vertebræ:

	M.		M.
Length of centrum of sharp keeled dorsal	0.014	of rounded dorsal	0.012
Depth behind	0.012		0.011
Width behind	0.012		0.0105.

Cope says of Clepsydrops: "This genus is more typically Rhynchocephalian than Cricotus," not knowing at that time that Cricotus is one of the Stegocephali (Labyrinthodonta).

The next communication was made by Cope<sup>2</sup> in 1877. Clepsydrops is now placed definitely among the Rhynchocephalia. Clepsydrops collettii Cope is said to be the most abundant land vertebrate of the formation, being represented in all the collections, sometimes by portions of individuals of double the size of the type. There is a single occipital condyle. Two new species of Clepsydrops are described, C. vinslovii and C. pedunculatus.

C. vinslovii Cope is based on a third cervical vertebræ, and probably represented by other vertebræ. C. pedunculatus Cope is established on a third cervical and another, apparently dorsal one. This species is said to be characterized by the stronger diapophyses.

Teeth are described, Species No. 4, p. 56, and are referred to *Clepsydrops collettii*. The horizon from which the fossils came is now considered as Permian, and is named the *Clepsydrops shale*.

In the same year the discovery of Permian Reptiles in Texas was announced by Cope,<sup>3</sup> and other remains from Illinois are described. Lysorophus tricarinatus Cope is named and described. "Vertebræ amphicælian, perforated by the foramen chordæ dorsalis. Neural arch freely articulated to the centrum. Floor of neural canal deeply excavated. No processes nor costal articulations on the centrum, which is excavated by longitudinal fossæ. Centrum not shortened." From near Danville, Illinois. Based on two centra and a portion of a third. Another new genus and species is based on teeth: Archæobelus vellicatus, "Species No. 4," Cope, Proc. Amer. Philos. Soc., 1877, p. 192.

A new species of *Clepsydrops*, *C. limbatus*, is described from Texas. It is based on a vertebra with the following dimensions:

		MI.
Length of centrum		0.031
Diameter of centrum {	verticaltransverse	0.039
	transverse	0.033

In the May number of 1878 of the American Naturalist, published April 22, Cope<sup>4</sup> made some remarks about the homology of the chevron bones. He says: "The basal portions of the chevron bones are continued throughout the greater part of the vertebral column in the Permian genera Clepsydrops, Metarmosaurus and Epicordylus [Eryops], forming intervertebral elements to which I have given the name intercentra"—"The free elements of the cervical series of some reptiles are probably the same." Here the name intercentrum is introduced. In the same number of the Naturalist Cope<sup>5</sup> refers to Clepsydrops: "Clepsydrops has been found to have the canine and incisor teeth distinctly characterized. The ischia are immensely enlarged in an antero-posterior direction, forming a boat-shaped body.\* The neural spines of the lumbar and sacral regions are greatly elevated, indicating a fin like that of Basiliscus." Two new species are described, C. natalis and C. gigas, the latter of the size of the larger Mammalia.

In May, 1878, a paper by Prof. O. C. Marsh<sup>6</sup> appeared in the *American Journal* of Science on Permian fossils. In the beginning he states that "hitherto no Permian vertebrates have been identified in this country, although not uncommon in Europe."

He continues: "The Museum of Yale College contains an extensive series of Reptilian remains belonging to a peculiar lacustrine fauna, which includes also Amphibians and Fishes. These fossils are from several localities in the West, but mainly from New Mexico, and the geological horizon appears to be in the upper portion of the Permian. These Reptilian remains are in excellent preservation, and among them are several general having the more important characters of the Rhynchocephalia, of which the genus Hatteria, of New Zealand, is the living type. The principal points of agreement are the separate premaxillaries, the immovable quadrate, and the biconcave vertebræ. Another character of much interest is the presence of certain hypaxial elements of the vertebræ, first observed by Von Meyer in the Triassic genus Sphenosaurus, and called by him intercentral bones ('Zwischenwirbelbein'). These wedge-shaped bones are apparently the homologues of the cervical hypapophyses in the Mosasauria, and of the subcaudal attachments in the Odontornithes, and a few recent birds. These intercentral ossifications apparently exist in all the Reptilia yet found in this new fauna, and hence serve to distinguish it. With this character is another of hardly less interest. The anterior ribbearing vertebræ preserved have three separate articular facets for the ribs, one on the

<sup>\*</sup>This pelvis probably belongs to Eryops.

anterior part of the centrum for the head, and a double one above for the bifid tubercle. In the implantation of the teeth and their successional development these Reptiles resemble the Mosasauria. These characters, with others mentioned below, indicate two distinct families, which may be called *Nothodontidæ* and *Sphenacodontidæ*, from the typical genera here described.

## "Nothodon lentus, gen. et sp. nov.

"This genus of Reptiles may readily be distinguished by the dentition. In each separate premaxillary there are two slender pointed teeth. In front of the maxillary there are one or two similar teeth, followed by a number with narrow transverse crowns, resembling in form the premolars of some carnivorous mammals. These crowns, when unworn, have a central cusp, and on each side a tubercle, somewhat like that on the premolars of the genus *Canis*. In the present species the first and last of the transverse teeth are smaller than the middle ones. The limbs were short, the long bones had their extremities covered with cartilage, but the carpals and tarsals were well ossified. The centra were very deeply concave, and the tail was long.

"The following measurements are taken from the type specimen of this species:

	MM.
Length of maxillary bone	. 65
Space occupied by ten maxillary teeth	. 55
Height of crown of second maxillary tooth	. 14
Height of crown of third maxillary tooth	. 9.
Antero-posterior diameter	. 3.
Transverse diameter	. 8
Antero-posterior diameter of eighth tooth	. 5
Transverse diameter	. 15.

"The present species was about five or six feet in length, and herbivorous in habit. It was apparently slow in movement, and probably more or less aquatic. The remains at present known are from New Mexico."

This is one of Cope's Diadectida.

## "Sphenacodon ferox, gen. et sp. nov.

"In the present genus the anterior teeth are somewhat like those of the reptile described above, but the posterior, or more characteristic ones, are totally different. The crowns are much compressed, and have very sharp cutting edges, without crenulations. In the present species the carnivorous teeth are crowded together, and the crowns placed slightly oblique, and twisted. The jaws were comparatively short and massive. The

rami of the lower jaws were apparently united by cartilage only, and the symphysis was short. The vertebræ are deeply biconcave.

"Measurements from the type of this species are as follows:

	MM.
Length of dentary bone	150
Space occupied by teeth	130
Extent of four anterior caniniform teeth	. 25
Extent of twenty compressed teeth	105
Height above jaw of second lower tooth	. 15.
Depth of dentary bone at symphysis	. 26.
Height of crown of compressed tooth	. 8.
Transverse diameter	. 4.

"This reptile was about six feet in length, and carnivorous in habit. Its remains are from the same locality in New Mexico that yielded those of *Nothodon*."

This is probably one of the Clepsydropidæ.

## " Ophiacodon mirus, gen. et. sp. nov.

"A third genus of Reptiles allied to the last described is indicated by various well-preserved remains from the same locality. The teeth are all carnivorous in type, conical in form, and all are similar. Those in the anterior part of the jaws are recurved, and in general shape resemble those of Serpents. The rami of the lower jaws were united only by cartilage. The vertebræ are very deeply biconcave, and even perforate, and the intracentral bones large. In the present species the teeth are nearly smooth, and somewhat compressed.

"The following measurements indicate the size of this reptile:

	MM.
Extent of anterior sixteen teeth in dentary	. 75
Extent of anterior five lower teeth	. 20
Height of crown of fourth lower tooth	
Depth of lower jaw at symphysis	. 15
Extent of seven anterior maxillary teeth	. 33.
Height of crown of first maxillary tooth	. 9.
Antero-posterior diameter of crown	. 3.

"This species was about as large as those described above, and is from the same geological horizon in New Mexico.

## "Ophiacodon grandis, sp. nov.

"A second larger species of apparently the same genus is represented by portions of the jaws, and teeth, and various parts of the skeleton. In this species the dentary bone is angular at its anterior extremity, and triangular in section. Its external surface is

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rugose, as in the Crocodiles. The crowns of the teeth are striate at the base, and the latter is furrowed vertically. The teeth are not so thickly set as in the smaller species, and the bases of the crowns are somewhat transverse.

#### " Measurements.

	MM.
Space occupied by ten anterior lower teeth	140
Depth of lower jaw at symphysis	129
Antero-posterior extent of symphysis	25.
Depth of dentary bone below seventh tooth	30.
Width of dentary at this point	20.

"The present species was about ten feet in length, and the largest reptile yet found in this fauna. The remains are from New Mexico."

The Ophiacodon mirus is one of the Clepsydropidæ, and O. grandis might be Eryops Cope.

The families "Nothodontida" and "Sphenacodontida" are, like the genera, established without diagnosis.

To this paper Cope<sup>7</sup> replied in *The American Naturalist*, June, 1878. He says that the four species of reptiles are characterized by Marsh in a very insufficient manner. He should not regard his article as suitable for notice in The Naturalist but for certain assertions which it contains, and some circumstances connected with its publication. The assertion that "hitherto no Permian vertebrates have been identified in this country, although not uncommon in Europe," he declares the reverse of the fact, referring to his paper in the Proceedings of the Academy of Natural Sciences of Philadelphia for 1875, pp. 393-424, where some of the leading characters of the reptiles are pointed out; to his papers in the Proceedings of the American Philosophical Society for May, 1877, pp. 52-63, where several new species are described, and in the same journal for November, 1877, in which other species are added, making the whole number up to twenty-one. He then continues: "These papers Prof. Marsh has had the opportunity of seeing. Two further notices of the vertebrates of the American Permian appeared on April 22, of the present year (1878), in the May number of this journal, pp. 319 and 327. As the corresponding number of the Am. Journ. Sci. and Arts was not issued before May 5 (perhaps a day or two sooner), Prof. Marsh had the opportunity of seeing these also. They include references to seven new genera, for most of which the characters are clearly pointed out.

"The features common to the genera of the Permian, described by Marsh, are stated by him to be those characteristic of the order *Rhynchocephalia*; as I have already shown to be the case with the forms described by me in the earliest as well as later papers of those cited. Another characteristic is said to be the presence of the intercentrum, a statement agreeing with my own in the May number of this journal.

"As the author of the paper does not think it necessary to allude to published sources of information, it is too much to expect him to give credit for ideas communicated to him verbally. All of the above mentioned and additional characters cited by Marsh in his ' two opening paragraphs as belonging to the Permian Reptiles, with others, were explained by me before the National Academy of Sciences, with Prof. Marsh as an attentive listener, at its last meeting in Washington, April 18, more than two weeks before the appearance of the paper here criticised. The characters to which I refer are 'the separate premaxillaries, the immovable quadrate and the biconcave vertebræ; the 'hypaxial elements of the vertebræ, called [by von Meyer] intercentral bones.' 'These intercentral ossifications apparently exist in all the Reptilia yet found in this new fauna.' Compare these statements with those found in my paper read before the National Academy (which had been previously read before the American Philosophical Society, April 5) and published May 8, and that Prof. Marsh profited by what he heard is evidenced by his use of the term 'intercentra,' first introduced by myself. From this point of view it is easy to understand his attempt to make it appear that Meyer first used the word. He says, 'Another character of much interest is the presence of certain hypaxial elements of the vertebræ, first observed by von Meyer in the Triassic genus Sphenosaurus, and called by him intercentral bones (Zwischenwirbelbein)' (sic). 'As Zwischenwirbelbein does not mean intercentrum, but intervertebral bone, Prof. Marsh's knowledge of the former term must be ascribed to some other source. The fact that the Amer. Journ. Sci. and Arts appeared a good deal later than its usual date of publication may be considered in this connection."

On May 8, 1878, appeared the first more extensive paper of Cope on the forms from the Permian of Texas. The following new genera and species were described: Diadectes sideropelicus and D. latibuccatus; Bolosaurus striatus and B. rapidens; Pariotichus brachyops; Ectocynodon ordinatus; Dimetrodon incisivus; D. rectiformis and D. gigas; Epicordylus erythroliticus; Metarmosaurus fossatus; Empedocles alatus; Embolophorus fritillus; Theropleura retroversa, T. uniformis and T. triangulata. A new species of Clepsydrops, represented by numerous portions of the skeleton, was established—C. natalis. The skull is described: "There is no quadratojugal arch, but the zygomatic and postorbital arches are present. The squamosal extremity of the zygomatic arch descends low on the quadrate as in turtles, preventing mobility of the latter." "The symphysis of the mandible is short, and the premaxillary bones appear to be distinct. The teeth were of different sizes and the premaxillaries and canines are distinguished from the others by their proportions. All are subround in section, with more or less defined anterior and posterior cutting edges. The premaxillary teeth are larger anteriorly, diminish pos-

teeth are of medium proportion. There is no surface sculpture of the cranial bones." The vertebræ and intercentra, the greatly elevated neural spines in the lumbar and sacral regions are described, the humerus with the entepicondylar foramen and the ectepicondylar groove. The ilium, ischium and femur. In regard to the relationship of Clepsydrops, Cope makes the following remarks: "Of the general affinities of this genus it is only necessary now to state, that my reference of it to the Rhynchocephalia is confirmed. It differs from the recent species of the order in the absence of quadratojugal arch and the remarkably developed ischia. On this account I refer to Clepsydrops and its allies as a distinct suborder under the name of Pelycosauria."

The new genus Dimetrodon is larger than Clepsydrops. The dentition is similar to that genus. The roots of the teeth are long and are contained in deep alveoli. Between the premaxillary and maxillary is a deep emargination of the border of the jaws. There are but two incisor teeth, of which the anterior is much larger than the second. The anterior two teeth of the maxillary bone are larger than the following ones, the anterior exceeding even the first incisor. The other maxillary teeth are smaller and subequal. The orbit is lateral, and has a prominent and convex superciliary border. The zygomatic arch is so curved upwards as to complete the orbit behind by the intervention of a postorbital or postfrontal bone, which separates the malar [jugal] and squamosal bones from mutual contact. In front of this bone a portion of the frontal forms the superciliary border, and in front of this, the prefrontal sends a wide process behind the lachrymal to the orbit. This bone resembles a nasal bone in form, and extends forward, and is decurved at the extremity. The width of the descending or malar process of the postfrontal is such as to partially separate the orbit from the zygomatic fossa. The superciliary surface is swollen, and is interrupted by a transverse groove on the orbital part of the prefrontal. There is a vertical open groove on the malar process of the postfrontal. Some pelvic bones are referred here. They include both the ilia, ischia and pubes in one mass, forming a compressed boat-shaped body, with a prominent inferior keel. They probably belong to Eryops.

Dimetrodon is said to be allied to Deuterosaurus Eichw. and Eurosaurus Fisch., as defined by Meyer. "Deuterosaurus has much more elevated nostrils, more numerous incisor teeth, and wants the extensive diastema in front of the superior canine. Lycosaurus Owen, from the South African Trias, resembles it much more nearly, but does not present the greatly enlarged anterior incisor teeth of Dimetrodon."

The new genera and species, *Epicordylus erythroliticus* Cope and *Metarmosaurus* fossatus Cope, which are based on vertebræ, are considered closely related to *Dimetrodon*. The new genera, *Embolophorus*, with one species, *E. fritillus*, and *Theropleura*, with

three species, *T. retroversa*, *T. uniformis* and *T. triangulata*, all based on vertebræ, are also placed near that genus.

A peculiar genus, *Empedocles* [*Empedias*] alatus Cope, with additional hyposphene and hypanthrum articulations, is also described.

In addition to the type of humerus referred to *Clepsydrops*, Cope describes three other humeri, which represent three other genera which have been probably already named from crania or vertebræ. Nos. 1 and 2 are compared with that of *Eurosaurus*, but the epicondyles are more largely developed. No. 3 is considered as belonging to *Empedocles* [*Empedias*].

Prof. Cope concludes his paper with the following remarks: "The division Pelycosauria is established primarily on the genera Clepsydrops and Dimetrodon, but their cranial structures render it highly probable that Ectocynodon, Pariotichus and Bolosaurus belong to it. It is also probable that the genera, Empedocles [Empedias], Embolophorus and others determined from vertebræ belong to it, as the latter are frequently accompanied by pelvic bones of the type of that of *Dimetrodon*. All the genera known from teeth and crania are of carnivorous habit, excepting Bolosaurus and Diadectes; they may be referred to a single family on this account, which I call the Clepsydropsida. Bolosaurus will form the type of another family characterized by the transverse position of the crowns of the teeth, under the name of Bolosaurida. Prof. Owen has named a group of Triassic and Permian reptiles the *Theriodonta*, characterized by the mammal-like differentiation of the incisor and canine teeth. The animals thus referred by Prof. Owen probably enter my suborder of *Pelycosauria*, although the structure of their pelvis remains to be ascertained. If so, they correspond with my Clepsydropsida, since Prof. Owen does not include herbivorous forms in his division. As it is plain that the herbivorous and carnivorous types belong to the same order, and probably suborder, it becomes necessary to subordinate the term Theriodonta to that of Pelycosauria. To another division of reptiles from the South African Trias, typified by the genus Pareiasaurus Owen, he gives a special name, expressive of the deeply impressed surfaces of the centra occupied by the remains of the *chordæ dorsalis*. As this, or the perforate condition, is characteristic of all of the *Pelycosauria*, it is probable that it is present in Prof. Owen's Theriodonta also. It is also evident that since the dental characters of Pareiasaurus do not serve to distinguish it as an order from the genera with distinct canine teeth, this group also must be looked upon as a subdivision, perhaps of family value, of the Pelycosauria or other parts of the Rhynchocephalous order."

In regard to the geological formation of the Illinois and Texas beds, he comes to the conclusion that they are Permian.

On the 7th of November, 1878, Prof. Cope<sup>9</sup> read a paper before the National Acad-

emy of Sciences, at its meeting in New York, on the *Theromorphous Reptilia*. "He stated that he had determined that the scapular arch in the *Pelycosauria* consists of scapula, coracoid and epicoracoid, which form a continuum in the adult, in the same way as the three elements of the pelvis in the same group form an os innominatum. He showed that the tibiale and centrale of the tarsus unite to form an astragalus, which has no movement on the tibia. The fibulare forms a calcaneum. The distal side of the astragalus presents two facets, one of which receives a large part of the proximal extremity of the cuboid.

"The structure of the scapular and pelvic arches was stated to be identical with that already described by Owen as belonging to the *Anomodontia*. Several important characters distinguish this group from the *Pelycosauria*, but the two together form an order, which Prof. Cope thought would have, for the present at least, to be retained as distinct from the *Rhynchocephalia*. The characters of this order, with its two suborders, were given as follows:

"Theromorpha Cope. Scapular arch consisting at least of scapula, coracoid and epicoracoid, which are closely united. Pelvic arch consisting of the usual three elements, which are united throughout, closing the obturator foramen [f. pubo-ischiaticum] and acetabulum. Limbs with the phalanges as in the ambulatory types. Quadrate bone proximally united by suture with the adjacent elements. No quadratojugal arch.

"Pelycosauria. Two or three sacral vertebræ; centra notochordal; intercentra usually present. Dentition full.

"Anomodontia. Four or five sacral vertebræ; centra not notochordal; no intercentra. Dentition very imperfect or wanting.

"The *Rhynchocephalia* have no distal ischio-pubic symphysis, and apparently no epicoracoid bone. They have an obturator foramen [foramen pubo-ischiaticum] and a quadratojugal arch.

"The order Theromorpha was regarded by Prof. Cope as approximating the Mamma-lia more closely than any other division of Reptilia, and as probably the ancestral group from which the latter were derived. This approximation is seen in the scapular arch and humerus, which nearly resemble those of the Monotremata, especially Echidna; and in the pelvic arch, which Owen has shown in the Anomodontia to resemble that of the Mammals, and, as Prof. Cope pointed out, especially that of Echidna. The tarsus is also more mammalian than in any other division of reptiles. In the genus Dimetrodon the coracoid is smaller than the epicoracoid, as in Monotremes. The pubis has the foramen for the internal femoral artery."

At the end of this note a new species of *Dimetrodon* is described under the name of *D. cruciger*. "It is characterized by the enormous length of the neural spines of the

lumbar vertebræ, which form the dorsal fin seen in other species of the genus. In this species the spine sends off, a short distance above the neural canal, a pair of opposite short branches, forming a cross. At various more elevated positions there are given off tuberosities, which alternate with each other." This species of *Dimetrodon* was later made the type of *Naosaurus* Cope.

Cope's "Second Contribution to the History of the Vertebrata of the Permian Formation of Texas" appeared June 5, 1880. The general conclusions about the *Theromorpha* he had already published in the *American Naturalist*, December, 1878, which we have reviewed above. Cope now believes that the *Pelycosauria* are related to the *Amphibia* in some important respects (scapular and pelvic arches, humerus, dentition of palatal region), but he says: "In spite of these approximations, the *Pelycosauria* are distinctly reptilian in their single occipital condyle, ossification of the basi-cranial axis and single vomer."

"Thus the reptiles and batrachia of the Permian period resemble each other and the *Mammalia* more closely than do the corresponding existing forms."

The genus Theropleura is more fully defined from a better preserved specimen of Theropleura uniformis than any so far obtained. "The teeth are generally similar to those of Clepsydrops and Dimetrodon, having compressed crowns with fore and aft cutting edges. The incisors are distinguished by the presence of a diastema. Posteriorly to this the teeth increase in size and then diminish; one tooth near the middle of the series is the largest, but does not in this species very much exceed the others. There is at least one large incisor tooth. The bones of the head are smooth and not sculptured. The symphysis of the mandible is short." The neural arches are distinct from the centra. Intercentra are said to be absent in the thirteen vertebræ preserved; but there was probably one below the centrum of the atlas. The ribs are two-headed, the capitular process extending downwards to the anterior border of the centrum. The neural spines of some of the vertebræ are greatly elevated, as in the species of Clepsydrops and Dimetrodon. Dermal rods are said to be present, suspected to be abdominal, and this is considered a batrachian character. The neural spine of the axis is extended fore and aft. The odontoid is distinct and is of large size. It has lateral and inferior articular surfaces.

Theropleura uniformis is described to be of the size of the larger Varanidæ, and about equal to the Clepsydrops natalis. It is characterized by a long and acuminate head, with a large lateral nostril on each side, well forwards and approaching near the border of the diastema. Anterior to the large lateral tooth there are nine teeth; posterior to it there are eighteen. Length of alveolar edge of mandible 0.120 m.

A new species of Theropleura is described as T. obtusidens, represented by nearly

all parts of the skeleton, including jaws of both sides with teeth, numerous vertebræ and bones of the limbs.

The neural arches are coössified with the centrum. The jaws are long and slender and the teeth are of equal size. The number of teeth in the dentary is about twenty-one. The mandibular articular face consists of two open parallel grooves, one shorter than the other, extending obliquely to the long axis of the jaw. A dentigerous bone of the palate is described.

The vertebræ have simple elongated neural spines. Intercentra are indicated by the shape of the vertebræ, but not preserved. Traces of sutural articulation with the neural arches remain. Many of the centra are much compressed and have a narrow, sharp median keel.

Dimetrodon is more fully described; the vertebræ and a portion of the muzzle are figured. Parts of the palatopterygoid are described, probably pieces of the palate and pterygoid; both bear teeth. The posterior part of the skull displays typical reptilian characters. The occipital condyle is described as not perforated nor divided by sutures. The exoccipital bones [paroccipital processes] project well backwards. The lateral walls of the brain-case are massive as far forwards as the exit of the fifth pair of nerves; anterior to this point they were thin or wanting. The basisphenoid carries two parallel descending laminæ, which bound a deep median fissure, and then unite anteriorly. Posteriorly they abut on a descending process, which is followed by a lid-like element which is applied to a circular fossa with a raised border near the occipital condyle.

The articular face of the articular bone of the mandible consists of two parallel cotyli, divided by a ridge of articular surface. [This is the quadrate.] This part of the jaw is much depressed, as in *Eryops*. The large teeth of the lower jaw are at the anterior extremity. The neural spine of the axis is flat and elongate antero-posteriorly. From this point the neural spines rise rapidly in elevation until on the dorsal region they are many times as long as the diameters of the centra. Intercentra are present in the dorsals; and all the ribs are two-headed, from the axis. All the cervical and dorsal vertebræ have diapophyses with tubercular facets. The head of the rib is prolonged downwards and forwards to the prominent border of the anterior articular face, against which it abuts, but so far as yet observed without a corresponding facet. [The facet is on the intercentrum.] On the caudal vertebræ the two facets of the ribs are approximated and finally are not distinguished. They are here coössified with the centra. Then follow short notes on humerus, pelvis and femur.

Three species are distinguished as follows:

 The characters of *Dimetrodon cruciger* Cope, already given in *American Naturalist*, December, 1878, p. 830, are noted again.

A new genus *Helodectes* is established. It has the molar teeth in two series. Two species are named *H. paridens* and *H. isacii*.

In the American Naturalist of February, 1881, Prof. Cope<sup>11</sup> gave a list of the Vertebrates of the Permian Formation of the United States.

The following Reptilia are catalogued:

## Тнекомогрна Соре.

## Pelycosauria Cope.

Diplocaulidæ.

Diplocaulus salamandroides Cope, Eastern Illinois.

Clepsydropsidæ.

Pariotichus brachiops Cope, Texas.

Ectocynodon ordinatus Cope, Texas.

Archæobelus vellicatus Cope, Eastern Illinois.

" vinslovii Cope, Eastern Illinois.

" pedunculatus Cope, Eastern Illinois.

" natalis Cope, Texas.

Clepsydrops collettii Cope, Eastern Illinois.

Dimetrodon incisivus Cope, Texas.

" rectiformis Cope, Texas.

" biradicatus Cope, Texas.

" gigas Cope, Texas.

' cruciger Cope, Texas.

Theropleura retroversa Cope, Texas.

Theropleura uniformis Cope, Texas.

" triangulata Cope, Texas.

obtusidens Cope, Texas.

Metarmosaurus fossatus Cope, Texas.

Embolophorus fritillus Cope, Texas.

Lysorophus tricarinatus Cope, Eastern Illinois.

Bolosauridæ.

Bolosaurus striatus Cope, Texas.

Diadectida.

Diadectes sideropelicus Cope, Texas.

" phaseolinus Cope, Texas.

Empedocles alatus, Cope, Texas.

" latibuccatus Cope, Texas.

" molaris Cope, Texas.

Helodectes paridens Cope, Texas.

" isacii Cope, Texas.

The next paper of Cope<sup>12</sup> is "On Some New Bratrachia and Reptilia from the Permian Beds of Texas." A new species of *Dimetrodon* is described under the name of *D. semiradicatus*; based on premaxillary and maxillary bones. There are three teeth on each premaxillary; in the maxillary 17 or 18. The first premaxillary and third maxillary are of nearly equal size and are much larger than the others, the second premaxillary only approaching them. Besides, the clavicles of *Dimetrodon cruciger* are discussed and compared with the corresponding elements of the *Stegocephali*.

In November, 1884, Prof. Cope<sup>13</sup> published his fifth contribution to the knowledge of the Permian Vertebrates. A new species of *Clepsydrops*, *C. leptocephalus*, is described. "This species is represented by almost the entire skeleton, the principal deficiency being that of the scapular arch and the anterior limbs, with the phalanges of the posterior feet."

The bones of the skull are mostly preserved. The *quadrate* bones are rather short, and articulate above by squamosal suture with the squamosals, which overlap them pos-

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Each edge of the groove is produced forwards; the external for a considerable distance as an acuminate laminiform process, in the usual position of a quadratojugal bone. The pterygoids were probably placed much as in Empedias molaris Cope (Proc. Am. Philos. Soc., Vol. xix, p. 56, Pl. V). They send inwards a subtriangular plate from each side, which approach each other on the median line without touching, and the adjacent edges are somewhat decurved. The posterior edges are deeply concave on each side of the middle line, and, like the inferior edges, are dentigerous. The process for the quadrate extends outwards and backwards, and is thickened on its posterior edge, while its anterior edge, which is continued from the inferior edge of the posterior border, becomes very thin. The anterior production for the ectopterygoids extends outwards and forwards, leaving the anterior edge of the dentigerous plates as the concave posterior border of the large palatine foramina. The anterior production of the internal edge of the plate becomes very thin, and is broken in the specimen without showing articulation for the palatine.

The squamosal extends both above and below its anteriorly directed zygomatic portion. The superior extremity shows squamosal suture for the parietal. The stapes (Pl. I, Fig. 2, a, b, c, d) is of large size. It consists of a stout rod terminating in a double extremity, something like the double head of a rib. The shorter head is expanded into a funnel shape. Near to it the shaft is perforated in the longer diameter by a foramen. The extremity of the other head is transversely truncate, and is separated from the funnel by a deep notch. On the outer side of the fundus of this notch a foramen penetrates the shaft obliquely, and is continued into a canal which issues at the foramen first described. The distal end is truncated by an irregular sutural surface. The premaxillaries are distinct. The teeth of that bone and of the maxillary are of unequal size.

The axis has an expanded neural spine and a diapophysis for rib articulation, but no parapophysis or capitular fossa. Behind the axis follow twenty-six vertebræ in a continuous series. All bear diapophyses, and all are rib-bearing, except perhaps the last two, where they are of reduced size. They are more or less opposite the neural canal as far as the twenty-second centrum. On this centrum the superior edge is on a level with the floor of the canal, and posterior to this point the diapophyses rise from the centrum. Two sacrals and ten caudals are preserved. The intercentra are short and not extended upwards on the sides. The neural spines were probably not elongated, as in *Dimetrodon*, though they are unfortunately broken off.

A new species of *Clepsydrops*, *C. macrospondylus*, is described, much exceeding *C. natalis* in dimensions. The dentary bone supports one or two large teeth near the extremity. There are preserved the axis, twelve continuous dorsals, nine other continuous vertebræ, of which three are lumbar, two sacral, and four caudal. Intercentra are

present. The centra are strongly compressed, and on the anterior part of the column have an obtuse hypophysial keel. The intercentra display equal width on the inferior surface, and are abruptly rounded at the extremities. The last one preserved is between the second and third caudal centra. The sacrum is rather robust. The sacral vertebræ are free, have well-developed neural spines and large free ribs for the ilium.

A new species of *Edaphosaurus*, *E. microdus*, is described. The genus *Edaphosaurus* was established on *E. pogonias*, represented by a specimen, which included only a distorted cranium. The new species is based on numerous vertebræ and ribs and the dentigerous plates of both jaws. The vertebræ possess enormously elongated neural spines as in *Dimetrodon*. The centra have a facet on the anterior edge above the middle for the head of the rib, as in a mammal. It is not repeated on the posterior edge of any of the thirteen centra preserved. The ribs are only compressed proximally. Distally their section is a wide oval.

The centra are rather elongate, and the foramen chordæ dorsalis is rather large. No intercentra are preserved, and if present they must have been very small, as the inferior rim of the centrum is not beveled to receive one. The neural spines have transverse processes which commence near the base, and project at intervals from the sides.

A special portion of the paper treats the *posterior foot* in the *Pelycosauria* (*Clepsydrops natalis*, Pl. I, Figs. 5, 6).

The astragalus and calcaneum are large and well-specialized bones free from each other and the other tarsal elements. The navicular is distinct. There are four tarsals in the distal series. Three are articulated with the metatarsals 1 to 3, the fourth with metatarsal 4 and 5. These elements are tarsal 1 (entocuneiform), tarsal 2 (mesocuneiform), tarsal 3 (ectocuneiform), and tarsal 4 and 5 (cuboid). There is a face on the astragalus for another element, which Cope thinks might have been a spur, as in the Monotremata.

The following conclusions are reached:

"1. The relations and number of the bones of the posterior foot are those of the Mammalia much more than those of the Reptilia. 2. The relations of the astragalus and calcaneum to each other are as in the Monotreme *Platypus anatinas*. 3. The articulation of the fibula with both calcaneum and astragalus is as in the Monotreme order of mammals. 4. The separate articulation of the anterior part of the astragalus with the tibia is as in the same order. 5. The presence of a facet for the articulation of a spur is as in the same order. 6. The posterior-exterior direction of the digits is as in the known species of Monotremeta."

"Thus the characters of the posterior foot of the *Pelycosauria* confirm the evidences of Monotreme affinity observed by Prof. Owen and myself in the bones of the legs,

especially of the anterior leg. It remains a fact that with this resemblance in the leg there is a general adherence to the reptilian type in the structure of the skull." But this adherence is not so exclusive as has been supposed, as he endeavors to show.

An account is now given of the structure of the columella auris in Clepsydrops leptocephalus. The columella resembles a rib, of which the suprastapedial process resembles the head, and the stapes the tubercle. If this process be the incus, the stapes is shortened as in the majority of Mammalia. We have here an approximation to the Mammalia in two points: (1) The perforation of the head of the stapes; (2) and the ossification of the incus, which (3) is distinct from the malleus, thus furnishing homologues of the principal ossicles of the ear.<sup>14</sup>

The structure of the quadrate bone in the genus Clepsydrops is then discussed. This bone in Clepsydrops leptocephalus Cope, already described, is of highly interesting form. Its lower horizontal process is homologized with the zygomatic process of the squamosal bone of the Mammalia, forming with the malar bone the zygomatic arch. "In the Pelycosauria there is but one posterior lateral arch, as is demonstrated by many specimens; hence, we have here a reptile with a zygomatic arch attached to the distal extremity of the quadrate bone."

After this some remarks follow about the articulation of the ribs in Embolophorus. "The ribs of the Theromorpha are two-headed. While the tubercular articulation has the usual position at the extremity of the diapophysis, the capitular is not distinctly, or is but partially indicated, on the anterior edge of the centrum, in Clepsydrops and Dimetrodon. In Embolophorus, as shown in 1878, the capitular articulation is distinctly to the intercentrum." Therefore the ribs of the Theromorpha are intercentral and not central elements, and are homologues, according to Cope, of the chevron bones [!]. This type of rib articulation also approximates closely that of the Mammalia, where the capitular articulation is in a fossa excavated from two adjacent vertebræ.

Finally the origin of the Mammalia is discussed. The Mammals are considered as the descendants of the Pelycosauria, and a table shows the relations between the Amphibia, Pelycosauria, other Reptilia, and the Mammalia. The same results were published in the Proc. Amer. Assoc. Adv. Science, Vol. xxxiii, pp. 471–482, 1 Pl., Salem, 1885, with the title, "The Relationships Between the Theromorphous Reptiles and the Monotreme Mammalia." In April, 1885, Prof. Cope published a paper "On the Evolution of the Vertebrata, Progressive and Retrogressive." Here he derives all Reptilia, with the possible exception of the Ichthyosauria, from the Theromorpha.

In April, 1886, Cope<sup>17</sup> gave figures of the vertebræ of *Clepsydrops natalis* Cope. In June of the same year he established the genus *Naosaurus*, in a paper with the title,

"The Long-spined Theromorpha of the Permian Epoch." Referring to Dimetrodon he says:

"The huge neural spines formed an elevated fin on the back. In a medium-sized specimen of Dimetrodon incisivus, where the vertebral body is 35 mm. in length, the elevation of the spines is 900 mm., or twenty and a half times as great. The apex of the spine in this species is slender, and apparently was flexible. The utility is difficult to imagine. Unless the animal had aquatic habits, and swam on its back, the crest or fin must have been in the way of active movements. Accordingly the spines are occasionally found distorted at the union of the faces of fractures. The limbs are not long enough nor the claws acute enough to demonstrate arboreal habits, as in the existing genus Basilicus, where a similar crest exists. A very peculiar species has been described under the name of Naosaurus claviger Cope. There the spines are not quite so elevated as in the D. incisivus, but they are more robust, and have transverse processes or branches which resemble the yardarms of a ship mast. In a full-sized individual the longest crossarms, which are the lowest in position, have an expanse of 260 mm., or ten and a quarter inches, while the spine has about the height of 500 mm. (19.75 in.), the body being 60 mm. long. The animal must have presented an extraordinary appearance. Perhaps its dorsal armature resembled the branches of shrubs then, as they do now, and served to conceal them in a brushy or wooded region; or, more probably, the yardarms were connected by membrane with the neural spine or mast, thus serving the animal as a sail with which he navigated the waters of the Permian lakes. A very singular character of the spines in all the species is that they are hollow, as in Coelacanth fishes, and that the central cavity is not closed at the apex.

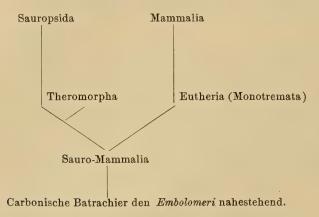
"There is a well-preserved cranium of the *D. claviger*, but the muzzle is unfortunately wanting. The median line rises forward so that the convexity of the top of the muzzle is higher than the posterior parts of the skull, whose profile descends rapidly. This throws the orbit far back, and gives the animal a peculiar appearance. *Naosaurus* differs from *Dimetrodon* in the transverse processes of the neural spines of the vertebræ. There are three species, which differ as follows:

"All these species are from the Permian formation of Texas."

In a paper by Baur<sup>19</sup> on the humerus of the Amniota, published in 1886, a few remarks are made on the relationship of the Theromorpha and the Mammalia. Baur

says: "Cope betrachtet die Pelycosauria als die Ahnen der Säugethiere. Ich glaube jedoch, dass dieselben schon etwas zu stark specialisirt sind, um diesen Anforderungen entsprechen zu können.

"Darüber aber kann kein Zweifel sein, dass die Pelycosauria den Stammaltern der Säugethiere sehr nahestehen. Beide sind vielleicht aus derselben Gruppe hervorgegangen, einer Gruppe, welche zwischen den Batrachiern und Reptilien des Perm in der Mitte stehen würde, und welche ich Sauro-Mammalia nennen möchte. Folgendes Schema möge den Zusammenhang ausdrücken:



A new catalogue of Permian vertebrates was published by Cope<sup>20</sup> in October, 1886.

## The romorpha.

Clepsy dropid a.

? Lysorophus Cope, 1877.

L. tricarinatus Cope, 1877, Eastern Illinois. Archaobelus Cope, 1877.

A. vellicatus Cope, 1877, Eastern Illinois. Clepsydrops Cope, 1875.

C. collettii Cope, 1875, Eastern Illinois.

C. vinslovii Cope, 1877, Eastern Illinois.

C. pedunculatus Cope, 1877, Eastern Illinois.

C. natalis Cope, 1878, Texas.

C. macropondylus Cope, 1884, Texas.

C. leptocephalus Cope, 1884, Texas.

[C. limbatus Cope, 1877, Texas, not mentioned] Dimetrodon Cope, 1878.

D. gigas Cope, 1878, Texas.

D. incisivus Cope, 1878, Texas.

D. rectiformis Cope, 1878, Texas.

D. semiradicatus Cope, 1878, Texas.

Naosaurus Cope, 1886.

N. cruciger Cope, 1878 (Dimetrodon), Texas.

N. claviger Cope, 1886, Texas.

N. microdus Cope, 1884 (Edaphosaurus), Texas.

Theropleura Cope, 1878.

T. retroversa Cope, 1878, Texas.

T. uniformis Cope, 1878, Texas.

T. triangulata Cope, 1878, Texas.

T. obtusidens Cope, 1880, Texas.

Embolophorus Cope, 1878.

E. fritillus Cope, 1878, Texas.

E. dollovianus n. sp. Cope, 1886.

Edaphosaurus Cope, 1882.

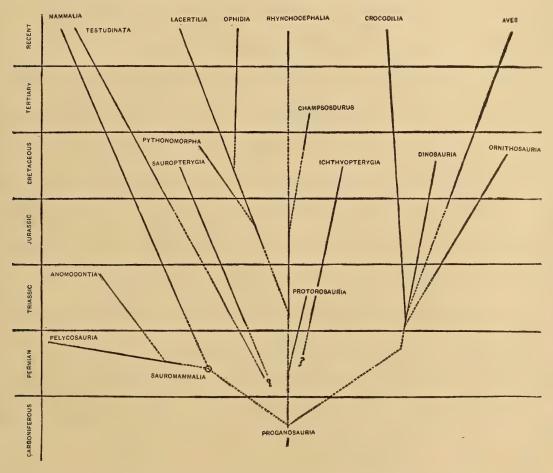
E. pogonias Cope, 1882.

Remarks are made about Dimetrodon and Naosaurus.

"In a medium-sized specimen of *Dimetrodon incisivus*, where the vertebral body is 35 mm. in length, the elevation of the neural spine is 900 mm., or twenty and a half times as great." The interclavicle is described as *sternum* and figured Pl. III, Fig. 5. A posterior foot of *Theropleura* (spec.?) is figured and described.

Naosaurus differs from Dimetrodon in the presence of transverse processes on the neural spines. Portions of the skull and vertebræ of Naosaurus claviger are described and figured (Pl. II, Figs. 1–3; Pl. III, Fig. 1). Vertebræ of Naosaurus cruciger and N. microdus are also figured (Pl. III, Figs. 2 and 3).

In 1887 Baur <sup>21, 22, 23</sup> gave the following diagram to express the relationship between the *Theromorpha*, the other Reptiles and the Mammals:



Lydekker in 1890<sup>24</sup> describes some Pelycosaurian remains from the Permian of Texas in his "Catalogue of the Fossil Reptilia and Amphibia in the British Museum," Part IV.

1. Pieces of the maxilla and neural spines of Naosaurus cruciger Cope. 2. Portions of spines of Naosaurus claviger Cope, and of undetermined species of Naosaurus. 3. Two dorsal vertebræ and an intervening intercentrum of Embolophorus spec. 4. Two dorsal

vertebræ and an intercentrum, and two other portions of dorsal vertebræ of *Embolo-phorus dolloverianus* Cope.

The next paper to be mentioned is by Prof. Cope,<sup>25</sup> "On the Homology of the Posterior Cranial Arches in the Reptilia," published in April, 1892.

Clepsydrops leptocephalus Cope is made the type of a new genus, Diopeus Cope. The following species have well-preserved crania which display sutures: Chilonyx rapidens Cope; Pantylus cordatus Cope; Pariotichus megalops Cope; Edaphosaurus pogonius Cope; Clepsydrops natalis Cope; Naosaurus claviger Cope; Diopeus leptocephalus Cope.

"The genera *Chilonyx*, *Pantylus* and *Pariotichus* have the temporal fossæ entirely roofed over, thus belonging to the *Cotylosauria*, to which must be probably referred the genus *Pareiasaurus* Owen, of the South African Karoo formation, and the *Phanerosaurus* of the German Permian. The other genera, excepting *Diopeus*, belong to the *Pelycosauria*, which is probably the same as the *Theriodontia* of Owen.

"Chilonyx agrees with the Stegocephalia and with other Diadectidæ in possessing a distinct os intercalare [epiotic aut.; paroccipital plate, Baur,<sup>26</sup> 1889; os tabulare or tabular bone, Cope,<sup>27</sup> 1894]. The component elements of the cranial roof are equal in number and similar in position to those of the Stegocephalian skull, except that the supramastoid [squamosal] extends between the parietal and intercalare [paroccipital plate] to the posterior border of the cranial table (Fig. 2, Sm.); and the supraoccipital does not extend on to the superior face of the skull, except as a narrow border. The quadrate bone is directed forwards instead of posteriorly, which causes an antero-posterior abbreviation of the supratemporal [prosquamosal] and squamosal elements. The elements of the temporal roof are not exclusively tegumentary, but are identical in character with the bones of the brain case, and the sutures are visible on the under as well as the upper side.

"Pantylus agrees with Chilonyx in the composition of its cranial roof with the exception that the suspensorium is vertical and is not directed forwards" (Fig. 4, Pl. I).

"Pariotichus Cope agrees in the main with Chilonyx, but the supraoccipital is divided medially and is reflected on to the superior face of the skull as in Stegocephali. The intercalare [paroccipital plate] is reduced to a small element, of which a small part appears on the superior face of the skull immediately behind the exterior part of the supramastoid" [squamosal] (Fig. 3, Pl. I).

Then it passes to the *Theriodontia* (*Pelycosauria*).

In "Naosaurus Cope (Fig. 7, Pl. II), the orbit is in the posterior part of the skull and the muzzle is greatly elevated and compressed [?]. The zygomatic (quadratojugal) is greatly decurved posteriorly and the supratemporal [prosquamosal] is accordingly decurved also. The postfrontal (Fig. 7a) is a narrow bone, wider than long, and it has connection with the frontal, parietal and postorbital only. The postorbital is an L-shaped

structure, of which the shorter limb is inferior, extending to the jugal, while the longer limb is posterior, extending to the supratemporal [prosquamosal], in contact with the parietal. It encloses no foramen with the latter; but it encloses a larger foramen with the jugal, zygomatic [quadratojugal] and supratemporal [prosquamosal] at the other boundaries. This is the infratemporal foramen of Baur. Posterior to the parietal is a small transverse element, which appears to be merely adherent to the former. Its determination is not easy at present. The supratemporal [prosquamosal] is elongate vertically, and narrow antero-posteriorly. Beneath and towards the middle line of the skull is a part of another bone which may be the paroccipital, or even exoccipital. The pineal foramen is distinct. No parietoquadrate arch."

"In Clepsydrops the structure is apparently the same, although the form is much less modified. The quadrate articulation is nearly in line with the maxillary dental series (Fig. 6, Pl. II), and the jugal is nearly horizontal; its inferior border being concave upwards. No bar extends posteriorly from the postorbital, which joins the supratemporal [prosquamosal], enclosing with it the infratemporal foramen. No indication of a supratemporal foramen can be found in the rather mutilated specimen. I think it was not present."

"In Edaphosaurus Cope (Fig. 5, Pl. II), the skull is of a more depressed type than in the preceding genera. The postorbital is mainly preserved, and it is in contact with the frontal proximally, and sends out no bar posteriorly. There was apparently no supratemporal foramen, but a very large infratemporal, which extended well upwards. There is no parietoquadrate arch. An element, perhaps supraoccipital, terminates in a free compressed apex on each side of the median posterior region. This may be homologous with the small free bone described in Naosaurus, in nearly the same position. The stapes is very large, and is at least partially perforated near the expanded proximal extremity. It is probably fully perforated, as I have described it in the Diopeus leptocephalus Cope."

"In Diopeus Cope, the supratemporal is elongate in the vertical direction, and as elsewhere it overlaps the quadrate at the distal extremity. Anteriorly, it sends forwards a process probably for union with the postorbital bone, which is, however, entirely free from the parietal, and encloses a foramen with it, precisely as in Sphenodon. It further resembles the corresponding element in Sphenodon in sending upwards a branch for union with the parietal. Thus there are in this genus two posterior bars and two foramina, thus differing widely from the other Permian genera of this or any other country known to me. Whether it has a free parietoquadrate arch I do not know, but it is probable that the genus should be referred to the Rhynchocephalia, in the neighborhood of Palæohatteria Cred. It differs from Sphenodon and resembles closely the Theriodontia in the absence of an obturator foramen, and in the character of its dentition. The zygomatic

bone [quadratojugal] is not excavated below, but has a straight outline to its junction with the jugal. The quadrate condyle is double like that of *Sphenodon* and the *Clepsydropsidæ*" (Fig. Pl. II).

"The *Theriodonta* described by Owen appear to have the single cranial arch constructed in the same way as I described above as characteristic of the American forms. I gather this from Owen's figures of the genera *Kistecephalus* Ow., *Galesaurus* Ow., *Scaloposaurus* Ow., *Anthodon* Ow., and apparently *Lycosaurus* Owen."\*

The posterior region of the *Anomodontia* is then discussed. They possess an "extensive supratemporal foramen, and that the bone which bounds it externally consists posteriorly of the supratemporal bone [squamosal], and not the zygomatic [quadratojugal]. Anteriorly this bone joins the postorbital, postfrontal and malar" [jugal]. "It is evident then that the *Anomodonta* differ from the *Theriodonta* in the absence of a zygomatic [quadratojugal] arch, and in the presence of a supratemporal arch, which is separated from the parietal bone by a supratemporal foramen."

Prof. Cope thus reaches the conclusion that there are four types of crania represented in the Permian Reptilia, which he distinguishes as follows:

Temporal roof uninterrupted	ylosauria.
A zygomatic arch, but no distinct supratemporal or supramastoid arches The	eriodonta.
Zygomatic and supratemporal arches	peus.
No zygomatic; a supratemporal arch	omodontia.

Discussing the *parietoquadrate arch*, Prof. Cope remarks: "The parietoquadrate arch is a later appearance in geologic time. It is not present in any of the Permian orders."

In 1897, Baur and Case<sup>28</sup> showed that the *Pelycosauria* possess two temporal arches, an upper postorbito-squamosal and a lower quadratojugal arch, besides the parieto-quadrate arch. They also demonstrated that the *Pelycosauria* are specialized *Rhynchocephalia*, which die out during the Permian, and cannot be the ancestors of the *Mammalia*.

Shortly before his death, Prof. Cope<sup>29</sup> wrote a review of this paper with discussions, which was published in the *American Naturalist* of April, the last number he edited.

#### THE PELYCOSAURIA FROM THE PERMIAN OF FRANCE.

The first remains of Permian Reptiles, which we consider as Pelycosaurian, were described in 1856 by Coquant, 30 and later redescribed and figured by Gervais. 31

They consisted of an upper jaw of a Reptile, found near Moissey, which was considered by Coquant as belonging to *Protorosaurus*. It is preserved in the Museum of

<sup>\*</sup>Procolophon Ow. is also placed here.

Besançon. Gervais has examined these fossils and has given figures of them. "La pièce (Fig. 29) est longue de 0.065 m.; elle se compose d'un fragment considérable de la maxillaire gauche, portant une dent caniniforme suivie de huit cuitres dents plus petites et décroissantes dont la première est à quelque distance de celle qui par sa grandeur et sa forme peut être considérée comme une canine. Les dents sont comprimées, subcultriformes, trèsfaiblement striées longitudinalement, à bords antérieur et postérieur subtranchants, mais non denticulés en scie. Cette de ces dents qui occupe la position antérieure est aussi la plus grande et elle est comparable à une canine, distante de la première de celles qui suivent d'une longueur de 0.010. Sa hauteur, audessus du bord du maxillaire, est de 0.020, et sa longueur, à la base, de 0.007. La plus grande des dents qui la suivent n'a que 0.010 de fût. Les dents placées après celle-là vont en décroissant. On se rendfort bien compte de la disposition des dents placées en arrière de la canine et de leur grandeur décroissante par l'inspection de la contréempreinte du mème morceau (Fig. 30).

"On y voit, en avant de la canine, l'indice de quatre autres dents subégals entre elles, dont la quatrième, en comptant d'avant en arrière, est sensiblement écartée de la canine elle-même, comme l'est d'ailleurs la première des dents de l'autre série. Les dents étaient à peu près, triangulaires à leur couronne, et leur forme était assez peu différente de celle des dents placées en arrière de la canine. Les quatres empreintes de dents, celle de la canine et celles des huit dents qui suivent cette dernière, occupent ensemble, une ligne courb dont l'arc mesure 0.085."

Gervais denies the identity of this fossil with *Protorosaurus*; according to him it seems related to the *Geosaurs*, and he names it provisionally *Geosaurus* (?) cynodus.

It is evident that it is no crocodile; it can only be compared with the Pelycosauria. It seems to be different from *Stereorachis* Gaudry.

## Stereorachis dominans Gaudry, 1880.

The genus *Stereorachis*, from the Permian of Autun, was first described by Gaudry<sup>32</sup> in 1880. A more complete account with figures appeared in 1883.<sup>33</sup>

Of Stereorachis the following remains are preserved: The lower jaw about 135 mm. long is in very poor condition; thirteen teeth are present, the most anterior one is the largest. The maxillary is partially preserved, exhibiting nine teeth, the two first ones being the largest. The vertebræ were deeply biconcave, with the notochordal canal persistent. The clavicles and the interclavicle are Pelycosaurian in shape. The interclavicle especially resembles that of Dimetrodon as figured by Cope. Remains of scapula and coracoid are present and a number of ribs. The humerus is also typically Pelycosaurian. Very fine abdominal ossicles are preserved, showing that some Pelycosauria had a ventral plastron like Sphenodon, Palæohatteria and Kadaliosaurus.

Gaudry did not make any remarks about the relationships of *Stereorachis*. Zittel<sup>34</sup> in 1888 placed it among the *Stegocephali*: "Unterordnung Stereospondyli. Vollwirbler, l. Familie Gastrolepidoti, Bauchschupper." Lydekker<sup>24, 35</sup> was the first who gave the right position to *Stereorachis*, among the *Theriodontia* in the family *Clepsydropsidæ* Cope. Zittel<sup>36</sup> followed him in his Grundzügen der Paleontologie, 1895.

## Callibrachion gaudryi, Boule and Glengeaud.<sup>70</sup>

Callibrachion is the name applied to a very nearly perfect specimen from the Permian of Autun. It has many of the features of the Permian Reptiles and was compared by the authors with the Palwohatteria of Credner. That it belongs among the Pelycosauria there is little doubt, though the presence of procedus and opisthocedus vertebræ is an unwonted character in the group, and if their presence is established in the specimen may lead to a revision of its position. The authors say of the specimen, p. 15: "Le Callibrachion a beaucoup plus d'affinités avec le Reptile du Rothliegende de la Saxe que M. Credner a appelé Palwohatteria. D'après ce qui est conservé de la tête de notre spécimen, nous pouvons croire que les crânes des deux animaux étaient fort ressemblants. La division de la mâchoire inférieure en plusieurs éléments, la forme des dents, leur ordre de distribution suivant le grandeur à la mâchoire supérieure, sont des traits communs. Dans les deux fossiles les centrums étaient séparés des arcs neuraux, dépourvous d'apophyses transverses, et la notochorde persistait au centre des corps verté braux. Les pattes étaient également bien développées et disposées sur le même plan.

"Mais à la côté de ces ressemblances, nous pouvons notre quelques différences. Les vertèbres du *Callibrachion* présentent une procélie bien marquée et les premières vertèbres sont opisthocèles."

#### Pelycosauria from the Permian of Africa.

Owen<sup>37</sup> described in 1859 Galesaurus planiceps and Cynochampsa laniaria from the Beaufort Beds of the Karoo System and placed them in the family Crocodilia. In the final paper these Reptilian remains are figured but not referred to the Crocodilia. In the second edition of his Palæontology (1861) Owen<sup>38</sup> placed these two genera in a new, third family of the order Anomodontia, with the name Cynodontia. This is his classification:

#### Order Anomodontia.

- 1. Family Dicynodontia-Dicynodon Ow., Ptychognathus Ow.
- 2. Family Cryptodontia-Oudenodon Ow., Rhynchosaurus Ow.
- 3. Family Cynodontia-Galesaurus Ow., Cynochampsa Ow.

The family *Cynodontia* is thus characterized: "A pair of teeth in each jaw, resembling in shape, position and relative size to the other teeth, the canines of carnivorous mammals, and dividing the incisors from the molars."

Haeckel<sup>39</sup> in 1866 divides the *Anomodontia* into three families:

- 1. Rhopalodontia-Rhopalodon, Permian Russia.
- 2. Dicynodontia—Dicynodon, Ptychognathus.
- 3. Cryptodontia-Udenodon, Rhynchosaurus.

The order *Theriodontia* was established by Owen<sup>40</sup> early in 1876. It was to contain *Galesaurus* and *Cynochampsa* and the new South African genera *Lycosaurus*, *Tigrisuchus*, *Cynosuchus*, *Nythosaurus*, *Scaloposaurus*, *Procolophon*, *Gorgonops*, as well as the genus *Cynodraco*. He remarks:

"For the name of these extinct carnivorous Saurians I find it convenient and believe it will be generally acceptable to form a distinct order of Reptilia under the denomination of Theriodontia, with the following characters: Dentition of the carnivorous type; incisors defined by position, and divided from the molars by a large laniariform canine on each side of both upper and lower jaw, the lower canine crossing in front of the upper; no ectopterygoids; humerus with an entepicondylar foramen; digital formula of fore foot 2, 3, 3, 3, 3 phalanges."

In 1878 appeared Owen's Catalogue of the Fossil Reptilia of South Africa.<sup>41</sup> The Order Theriodontia is now defined in the following way:

"Char. Dentition of the carnivorous type; incisors defined by position, and divided from molars by a large laniariform canine on each side of both upper and lower jaws, the lower canine crossing in front of the upper as in Mammalia."

The *Theriodontia* are divided in three sections.

#### Section Binarialia.

The external nostrils are divided by a narrow partition; the entire skull has a compressed form.

Genera Lycosaurus Ow. Species L. pardalis Ow., L. tigrinus Ow., and L. curvimola Ow. Tigrisuchus Ow. Species T. simus Ow.

#### Fam. Mononarialia.

In this family of *Theriodontia* the external nostril is single or undivided, and the incisors exceed three in number in each premaxillary.

Genera Cynodracon Ow. Species C. serridens Ow., C. major Ow.

Cynochampsa Ow. Species C. laniarius Ow.

Cynosuchus Ow. Species C. suppostus Ow.

Galesaurus Ow. Species G. planiceps Ow.

Nythosaurus Ow. Species N. larvatus Ow.

Scaloposaurus Ow. Species S. constrictus Ow.

Procolophon Ow. Species P. trigoniceps Ow., P. minor Ow.

#### Fam. Tectinarialia.

Genus Gorgonops Ow. Species G. torvus Ow.

In 1881 Owen<sup>42</sup> described a new genus, *Ælurosaurus felinus*, from South Africa, which he considered as a member of the *Theriodontia*, belonging to the "Mononarial Section." The animal presents the elevated facial region of the *Pelycosauria*, with the convex alveolar border of the upper jaw and the posterior position of the orbits. The teeth are differentiated as in most all of the South African Reptiles. The posterior portion of the cranium is lost and was later restored by Seeley<sup>43</sup> as an elevated region. There is much more probability that it was depressed by the quick descent of the temporal bones to join the depressed quadrate as in the American forms. Only the skull of the form is known.

In this paper Owen adds certain characters to the order *Theriodontia*. He says: "To the characters of this order given in my *Catalogue of the Fossil Reptilia of South Africa*, viz., 'Dentition of the carnivorous type, incisors laniariform, canine on each side of both upper and lower jaws,' may now be added 'dentition monophyodont.' Add to these characters 'humerus perforated by an entepicondylar foramen.'"

In 1889 Seeley<sup>44</sup> discussed the whole group *Anomodontia* and their relations to the other Permian Reptiles. He says of the *Pelycosauria*, p. 282: "There are few data for judging of the systematic value of the *Pelycosauria*. But in view of the fact that the *Anomodontia* was originally made to include animals which are allied to the *Pelycosauria*, supposing that group to be well founded, it seems more in accordance with usage to class these animals with the *Anomodontia* than to adopt a new name like *Theromorpha* for a well-known ordinal type.

"There is need, however, that the distinctness of the *Pelycosauria* should be established. The tibiale and the centrale are said to unite to form an astragalus which has no movement on the tibia. One face of the astragalus receives the cuboid. Subsequently an entire carpus was figured, which has a very mammalian aspect. It is regarded as referable to *Clepsydrops natalis* Cope, and is classed as *Pelycosauria*. A similar tarsus was subsequently referred with doubt to the genus *Theropleura*. It is difficult to judge of its importance. Its characters appear to be more mammalian than those of the *Crocodilian* tarsus, for the bones of the distal row are completely ossified. The tarsus is absolutely unknown in any of the *Anomodontia* from Africa, Europe and Asia; and, therefore, there is no means of comparison with the American fossil.

"The *Pelycosauria* are said to have two or three sacral vertebræ, a notochordal column and intercentra usually present. With the evidence that *Dinosaurs* may have as few as two sacral vertebræ, as well as a larger number than has been found in any *Ano-*

modont, this ground of ordinal distinction fails. Similarly the mode of ossification of the intervertebral substance presents many types among the *Anomodonts*, one of which, already figured by Sir Richard Owen, might be regarded as notochordal. What the value of the intercentra may be I am unable to say, as they have not been figured; but intercentra, as I understand them, are not unknown among the *Anomodonts*.

"The remarkable vertebral column with the elongated neural spines referred to Dimetrodon is apparently unlike any known Anomodont, but the elongation of the neural spines in certain of the Wealden reptiles, like (?) Hylwosaurus, is not considered to militate against their position in the group to which they belong. And it may be doubted if the more extraordinary neural spine of Naosaurus, with its transverse branches, has any greater classificational value, since the transverse branches are the only characters by which the author separates Naosaurus from Dimetrodon. In Theropleura, which is also described as having elevated neural spines, abdominal rods are found. In a further discussion of the subject the author still considers Empedias as a member of the Pelycosauria."

In a scheme of classification given the *Pelycosauria* are regarded as a doubtful group near to *Lycosaurus* and *Dicynodon*.

In 1895 Seeley<sup>45</sup> divided the *Anomodontia* into three great divisions, the *Therosuchia*, *Therochelonia* and the *Mesosauria* or *Proganosauria*. The *Therosuchia* is defined as follows: "The palatine and the transverse bones of the palate are produced outwards and usually downwards, in an arch, which abuts against the inner side of the mandible. This character defines the group from the *Dicynodonts*, the *Mesosaurs*, *Nothosaurs* and all fossil groups of reptiles. There are more or less completely divided heads to the dorsal ribs. A foramen of variable size occurs between the ischium and the pubis. The ilium extends on both sides of the acetabulum."

The classification here given is as follows:

## "Therosuchia comprise:

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Pareiasauria.
Procolophonia.
Gorgonopsia.
Dinocephalia.
Deuterosauria.
Placodontia.
Theriodontia
\begin{cases} Lycosauria. \\ Cynodontia. \\ Gomphodontia. \end{cases}
Endothiodontia.
Theromora
\begin{cases} Pelycosauria. \\ Cotylosauria. \end{cases}
Kistecephalia.
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"Therochelonia comprise:

Dicynodontia.

"Mesosauria or Proganosauria:

Nothosauria (?)"

In a footnote the author says of the *Theromora*: "This group has no authority at present and is subject to future definition."

#### Pelycosauria from the Permian of Russia.

In 1838 Kutorga<sup>46</sup> reported the discovery of vertebrate remains on the west slope of the Ural mountains. He considered the remains to belong to mammals and thought that the rocks were of Carboniferous age. Several genera were described, *Brithopus*, *Orthopus* and *Syodon*.

In 1841 Fischer de Waldheim<sup>47</sup> described from the same locality a new genus, *Rophalodon*, which he characterized as follows: "Gesteilte Zähnen mit hohlen Stielen und mit soliden keulenformiger Krone. R. Wagenheimi, mit vorn gehielten Zähne, der kiel gezähnte. R. Mantelli, mit langsgefurchten Zähne."

In 1842 the same author described a second genus,<sup>48</sup> Eurosaurus, from the same material that had been used by Kutorga in his description of Orthopus.

In 1845 Wagenheim von Qualen<sup>49</sup> announced in a letter to Fischer the discovery of a specimen in the Russian deposits, which he considered a Carboniferous plant related to *Pecopteris*. This specimen was recognized by Fischer as a skull and described by him<sup>50</sup> in the *Bull. of the Soc. of Moscow* as *Dinosaurus Murchisonii*.

In 1848 Eichwald<sup>51</sup> more fully described the forms *Rhophalodon Wagenheimi* and *Dinosaurus Murchisonii*. The latter genus he regarded as a synonym of the first. Two new genera, *Deuterosaurus* and *Zygosaurus*, were described in the same paper.

In 1857–1858 Herman von Meyer<sup>52</sup> described a few forms from the Permian of Russia and later a second article discussed the same specimens more fully.<sup>53</sup>

In 1860, in his *Lethæ Rossica*, Eichwald<sup>54</sup> described all the known genera from the Russian Permian. He regarded all the Reptilian forms as belonging in two genera only, *Rhophalodon* and *Deuterosaurus*. He gave the following classification:

Fam. Theriodontisaurier.

Genus Deuterosaurus.
Rhophalodon.

Fam. Labyrinthodonten.

Genus Eurosaurus.

Zygosaurus.

Archægosaurus.

In 1880 Twelvetrees<sup>55</sup> discovered a skull and humerus in the same deposits from which the earlier Russian fossils had been taken. The skull was of a Labyrinthodont which he called *Platypodosaurus*, and the humerus he referred to Owen's *Theriodontia*.

In the same year the same author described<sup>56</sup> the genus *Cliorhizodon*, and two years later, in an article in the *Geol. Mag.*<sup>57</sup> described teeth referred to the genera *Cynodraco* and *Deuterosarus*.

In 1876 Owen<sup>58</sup> published a review of the Permian reptiles, in which he discussed most of the Permian forms.

In 1883 Trautschold<sup>59</sup> described the remains preserved in the collection of the University of Kasan. Two new genera were described, *Platyops* and *Trematina*.

In 1894 Seeley. discussed and figured the two principal genera of the Permian deposits of Russia, Rhophalodon and Deuterosaurus. He considered that of all the forms described from this region there are only two types. He says, p. 664: "The remains with a Theriodont dentition show two generic types, which are indicated by the skulls. They are defined as Rhophalodon (Fischer, 1841) and Deuterosaurus (Eichwald, 1848). Kutorga had previously founded Brithopus on the distal end of a humerus; Orthopus on the proximal end of a humerus; Syodon was based on a tooth. Fischer in 1847 separated Dinosaurus from Rhophalodon by dental and cranial characters. It is probable that the separation was based on sufficient evidence. And, although there is no conclusive association of parts of the skeleton to support the reference, it seems to me not improbable that Brithopus is identical with Deuterosaurus. That Orthopus includes Syodon, and the type of Rhophalodon, while the remainder of Rhophalodon corresponds with the genus Dinosaurus, as conceived of by Fischer."

These two forms he considers as belonging to the Anomodontia, but constituting a separate suborder described as follows, p. 715: "The Deuterosauria are defined as Anomodontia, distinguished from the other known groups by having (1) the palato-nares divided by the vomer and without having any hard palate extending over them. (2) The canine teeth are serrated (and large) with incisor teeth in front (in Deuterosaurus) and molar teeth behind. There are temporal vacuities and a pineal foramen. (3) There is no facet for the head of a rib on the (middle dorsal) vertebræ, and no proof that it was attached between any two centra in any vertebræ; the tubercle is attached to the transverse process. The lower dorsal ribs have no antero-posterior expansion. (4) There are two sacral vertebræ anchylosed. (5) The ilium has a small crest without conspicuous anterior development. The acetabulum is imperforate, as in the Dicynodontia and the Ornithosauria. The limbs and the shoulder girdle are strong. (6) The scapula is flat.

The two genera appear to be the types of two distinct families, *Deuterosauridæ* and A. P. S.—VOL. XX. E.

Rhophalodontidæ, distinguished by the structure of the temporal region of the skull, which has a median crest in the former, and is roofed over on the superior surface in the latter. In the former the incisor teeth are strongly developed; in the latter serrated, lanceolate molars are strongly developed behind the canines.

#### Deuterosaurus.

Has the skull compressed from side to side, with large transversely compressed incisor teeth. The lachrymal bone is greatly developed. The postorbital arch is deep, and situated below the orbit. The quadrate bone is large and developed below the foramen magnum on the type of *Placodus*. The vertebræ are biconcave. The ribs are long. The sacral ribs are well developed. The scapula is expanded at its free end. The pubis and ischium diverge from below the acetabulum; there is a supra-acetabular, articular wedge on the ilium.

## Rhophalodon.

Has the skull more elongate and less deep, with the superior temporal vacuities roofed with bone. The orbit is relatively far back and defended with a circle of sclerotic bones. The incisors are clearly evidenced. The canines are large. The lanceolate molar teeth are of the Megalosaurian type. The vertebræ are biconcave. The scapula is concave on its borders, without conspicuous expansion at the free end. The pubis and ischium do not manifestly diverge ventrally, there may be a supra-acetabular articulation on the ilium."

#### PELYCOSAURIA FROM THE PERMIAN OF BOHEMIA.

In the first volume of the Fauna of the Gascoal, Fritsch<sup>61</sup> described a specimen that he supposed to be a portion of the border of the pectoral fin of a fish. Later in a supplement to the third volume of the same work<sup>62</sup> he recognized the nature of the supposed spine and described it as the neural spine of new species of Cope's genus Naosaurus, N. mirabilis. This is the only reptile from the Permian deposits of the Bohemian region.

In 1895 Fritsch<sup>63</sup> described new forms from the same horizon. A figure of a dorsal vertebra and spine of the same species as before described is figured. There is no description beyond the statement of the length of the spine. "Dieselben besitzen eine 13fache Länge des Wirbelkörpers und erreichen eine Länge eines halben Meters." It is still considered as the single reptile of the horizon.

#### DESCRIPTION OF THE SKELETON OF DIMETRODON.

The general shape of the skull can best be seen from the figures. There are two temporal arches; an upper, postorbito-squamosal arch, and a lower quadratojugal arch. There is, of course, also a parietoquadrate arch.

Seen from above the following openings are found in the skull: The anterior nares, far in front, bounded by the premaxillaries, maxillaries and nasals; the orbits, placed nearly vertically, and surrounded by the frontals, prefrontals, lachrymals, jugals, post-orbitals and postfrontals; the supratemporal fossæ, bounded by the parietal, postorbital, prosquamosal and squamosal; the infratemporal fossæ, formed by the postorbital, jugal, quadratojugal and prosquamosal. The pineal foramen is placed between the parietals. The posttemporal fossæ are surrounded by the posterior parietal processes, the squamosal, the paroccipital processes and the supraoccipital.

The premaxillaries (Pl. I, Fig. 1) are small, strong, paired elements. They are suturally united in the middle line, sending a slender process between the nasals. Behind they are united with the maxillaries and at the union a deep notch is present. Their anterior edge is rounded and carried upon a slender recurved process which borders the nasal opening anteriorly and joins the nasals above. The lower portion of the opening is formed by the posterior part of the upper edge of the premaxillary, which is excavated at the base of the superior process. Internally the two bones unite at their anterior edges and show faces for the anterior ends of the vomers. There are three teeth in each premaxillary; the anterior large and strong, followed by two smaller ones. The nasals (Pl. I, Fig. 2n) are long and slender bones, connected with the premaxillaries, maxillaries, prefrontals and frontals. They are suturally united in the middle line, and diverging behind to enclose the pointed anterior ends of the frontals, which they overlie. Anteriorly they receive the posterior prolongations of the premaxillaries between them. Below they are united with the maxillaries and behind with the prefrontals. The frontals (Pl. I, Fig. 4) are paired. They are of peculiar shape. They form a very short suture with the parietals, reach in front between the posterior ends of the nasals and send out laterally slender processes which take part in the upper border of the orbit. The frontals are flat and narrow, showing that the skull was not very broad. They join the nasals, prefrontals, postfrontals and parietals. The parietals (Pl. I, Fig. 5) are very small and short. They are not suturally united with the supraoccipital, but by cartilage. Their posterior processes, which are first horizontal, but vertical at the distal end, join the squamosals. The parietals are connected with the frontals, postfrontals, postfrontals, squamosals, supraoccipital and paroccipital. The prefrontals (Pl. I, Fig. 3) are well developed; they take part in the anterior and upper border of the orbit. They join the frontals, nasals, maxillaries and lachrymals. The whole bone is bent upon itself at a right angle, producing an upper horizontal and lower vertical portion. The posterior

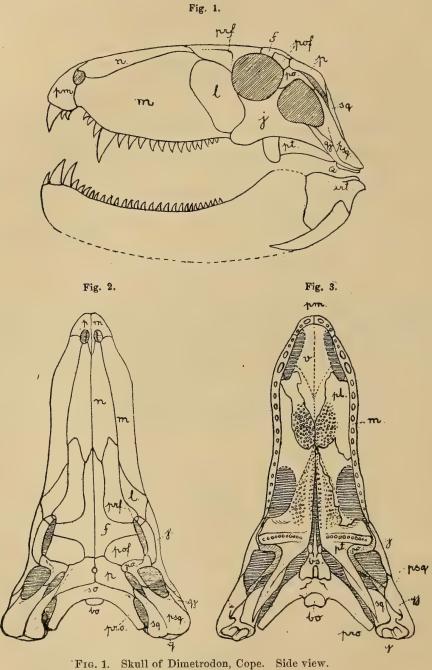


Fig. 1. Skull of Dimetrodon, Cope. Side view. Fig. 2. Skull of Dimetrodon, Cope. From above.

Fig. 3. Skull of Dimetrodon, Cope. From below.

edge is rounded and thickened, forming the upper anterior border of the orbital rim.

Just anterior to this there is a deep excavation, the preorbital pit. The bone becomes

quite thin, but there are no vacuities. The postfrontals bound the orbit above and are placed between the frontal, parietal and postorbital. They are approximately quadrangular in outline. Posteriorly they are joined to the postorbital by a broad flaring suture, the ridge thus formed marking the upper posterior angle of the orbital rim. The external edge, which forms part of the orbit, is thickened and rounded. The postorbitals (Pl. I, Fig. 7) take part in the formation of the orbit behind. They are united with the postfrontals and parietals above, send a posterior process to the prosquamosal. The postorbital is crescentic in outline, thin antero-posteriorly and expanded laterally. The jugal overlies a large part of the posterior surface of the lower portion and receives the lower end into a notch on its inner surface, so that the postorbital takes little part in the rim of the orbit, but forms a large part of its posterior wall. A deep groove extends on the external side between the faces for the postfrontal and jugal and notches the rim. The groove ends internally against a ridge which supports a long posterior process bearing the face for the prosquamosal. Internal to this ridge there is a flat slightly sigmoid face for the parietal.

The maxillaries are very large bones, very thin at the upper and lateral parts. They extend as thin plates far up on the side of the skull, reaching the lachrymals, prefrontals and nasals. They form a large part of the inferior and posterior border of the nasal openings. Below they become suddenly very thick to contain the deep alveoli of the teeth. This thickened portion takes the form of a strong ridge on the inner face of the lower edge and extends from the anterior end nearly to the posterior. The lower edge is gently convex downwards, anteriorly it is excavated by a deep notch, which marks the point of union of the maxillary and premaxillary. There are seventeen teeth in the maxillary. Two small ones occupy the maxillary part of the notch; succeeding this are two large teeth, one just appearing, and finally teeth nearly equal in size, but much smaller than the canine. The canine is directed nearly straight downwards, more convex on the outside than the inner and has well-defined anterior and posterior edges. The succeeding teeth are nearly uniform in size except the last few, which diminish rapidly. They are stout, quite strongly recurved and have strong antero-posterior cutting edges which are finely serrated. The maxillaries are joined with the premaxillary in front, the nasal and prefrontal above, the lachrymal and jugal behind; at the inner rounded and thickened lower part is found a very distinct suture for the palatines.

#### Measurements of Maxillary.

	M.
Length (nearly complete)	0.192
Length of largest tooth from base	0.055
Length of largest tooth from outer edge of jaw	0.040
Breadth of the same tooth at base	0.019
Length of fifth tooth from outer edge	0.018

The *lachrymals* are large plate-like and very thin except at their posterior extremity. Here the orbital portion is thickened and pierced by one or two foramina. Below, the edge becomes very thick and strong and is inserted into the posterior edge of the maxillary. The lachrymals form the anterior lower part of the orbit. They are joined to the prefrontals above, the maxillaries in front and below, the jugals behind.

The jugals (Pl. I, Fig. 6) are large and take part in the rim of the orbit, forming the lower and part of the posterior edges. The rim is marked by a sharp, elevated ridge. Below it is divided into two main parts. One running forwards and downwards joins the posterior edge of the maxillary. The inner face of this arm is marked by a strong ridge bearing at its lower edge a strong articular face for the ectopterygoid. The second runs almost straight backward, becomes quite slender posteriorly and joins the quadratojugal by a squamous suture. The whole of the lower portion of the bone becomes quite thin. The upper posterior process is united with the postorbital. The jugals join therefore the following elements: In front the lachrymals, below the maxillaries, behind the quadratojugals and above the orbitals.

The suspensorial region of the skull is composed of four elements: the quadrate, quadratojugal, squamosal and prosquamosal (Pl. I, Figs. 8, 9, 10).

The quadrate is peculiarly flat and depressed. It is covered superiorly by the squamosal, prosquamosal and quadratojugal. The squamosal, reduced distally to a broad, thin plate, is joined to the upper surface by a squamous suture, covering the inner portion. Laterally it wraps around the inner edge of the quadrate and appears largely on the lower face.

The outer part of the upper surface is covered by the prosquamosal and quadrato-jugal joining it by squamous suture. The prosquamosal lies just external to the squamosal, but is soon separated from the quadratojugal, which is wedged in between them. Superiorly the quadrate sends a process forward which extends between the squamosal and prosquamosal. The anterior end of this projection is incomplete, but possibly was continued forwards to join the posterior plate of the pterygoid. The outer edge of the projection is marked near its origin by a deep pit extending between the quadrate and quadratojugal. It represents the foramen between the quadrate and quadratojugal in Sphenodon, Phytosaurus (Belodon) and Ichthyosaurus.

The articular face for the lower jaw consists of two grooves lying at a large angle to the main axis of the skull. The outer is the longest and deepest, the inner wide and more shallow. They extend across the inferior face of the bone from before backwards, and are separated by a ridge as high as the external walls.

The quadratojugal, as shown by the articular face on the posterior process of the jugal, sent a strong process forwards. Posteriorly the inner edge extends as a wedge

between prosquamosal and the quadrate. On the inferior surface a strong process runs inwards and covers a part of the external edge of the quadrate. This process is notched by the deep pit already described. Anteriorly the bone became very thin and underlay the prosquamosal for quite a distance.

The *squamosal* joins the quadrate as already described. Externally it joins the prosquamosals, the two bones meeting with everted edges to form a narrow ridge. The cranial end of the squamosal was connected with the distal ends of the parietals by a narrow squamous suture.

The prosquamosal has been very largely defined in describing the other bones. The superior surface is marked by a prominent ridge, which curves forwards and inwards until it overhangs the ridge formed at the union of the squamosal and prosquamosal. The anterior process became very slender and narrow and joined the posterior prolongation of the postorbital, thus forming the upper temporal arch so characteristic for the Rhynchocephalia and the whole group of Archosauria.

The bones forming the *cranium* are all preserved, free from distortion and in their natural position. The whole region resembles *Sphenodon* in many particulars, but the obliteration of many of the sutures makes it impossible to compare exactly the separate elements (Pl. I, Figs. 11–14). The *cranium* is formed by the union of the basioccipital, exoccipitals, supraoccipital, the petrosals and the very large paroccipitals. The basisphenoid is completely free from the basioccipital. The connection was, without any doubt, by cartilage.

The basioccipital forms the lower half of the occipital condyle. The lower part of the condylar portion is rounded, and the upper comes to a sharp point between the exoccipitals. The point of union between the three bones is marked in some specimens by a deep pit, the anterior prolongation of the chordal canal. The lower surface is converted into a shallow groove by two descending flanges of bone. These meet laterally two other flanges from the paroccipitals, and the suture line is marked by a sharp constriction. Anterior to the trough described the lower surface of the bone rises at an angle of nearly ninety degrees. This face is excavated near its centre by a funnel-like depression, at the base of which lies the foramen for the Eustachian tube, as in the Crocodilia. This region is greatly swollen and contains the petrosals, though the sutures are entirely obliterated.

The *exoccipitals* form the borders of the foramen magnum, the basioccipital being excluded by their union below. The superior portions are very slender, and form only a narrow surface around the foramen. Inferiorly they become larger and form the superior half of the occipital condyle. They are pierced near their posterior edge by the condylar foramina.

The supraoccipital takes no part in the borders of the foramen magnum, being excluded therefrom by the union of the exoccipitals in the median line above the opening. It is somewhat triangular in outline, with the apex downwards. This is somewhat blunted and rests on the united exoccipitals. The sides join the expanded proximal ends of the paroccipitals. The superior border consists of a broad surface for cartilaginous attachment with the parietals.

The paroccipitals are very broad and massive proximally, but are produced in long distal processes. These processes project at a large angle from the posterior region of the skull and pass obliquely backwards, downwards and outwards. The distal articular surface is flat or slightly concave, oval in outline, and probably united to the quadrate by cartilage. The lower surface of these paroccipital processes is marked by two deep pits, separated by a sharp ridge. The proximal portion of the paroccipital is much expanded; above they are in union with the sides of the supraoccipital and bear at the superior edges winglike expansions for the parietals. Below they are suturally united to the exoccipitals and basioccipital. The lower portions of the proximal ends give rise to two descending flanges already described as joining the basioccipital. The region anterior to this flange is deeply excavated and open, so that the foramen rotundum and ovale are freely exposed.

# Measurements of the posterior cranial region.

	м.
Distance between distal ends of paroccipitals	0.122
Distance between ends of paroccipital processes	0.112
Breadth of foramen magnum	0.014
Height of foramen magnum	0.009
Breadth of occipital condyle	0.022
Height of occipital condyle	0.016
Distance from top of supraoccipital to lower edge of condyle	0.063

The basisphenoid (Pl. I, Figs. 13, 14) is broadly expanded posteriorly and contracts rapidly as it passes forwards, forming a neck just behind the closely approximated faces for the pterygoids, and ends anteriorly in a presphenoidal rostrum. The expanded posterior is marked on its upper edge by a pit, the continuation in the basisphenoid of the Eustachian canal. The centre of the posterior face is prolonged backwards in a spout-like process which lays in the groove described as marking the lower face of the basioccipitals. The lower edge of the expanded part is divided by a deep and long notch which ends abruptly anteriorly.

The basipterygoid processes are near the middle of the basisphenoid. They are short and stout, and in the natural position of the bone were nearly vertical, but directed slightly outwards, downwards and forwards. The upper part of the articular faces is

reflected backwards, forming small facets looking up and out. Between the pterygoid processes a slender presphenoid rostrum rises and projects far forwards. This rostrum is thin laterally, expanded vertically, smooth and straight on the lower edge, roughened above.

# The foramina perforating the cranial region and the brain.

The foramina penetrating the bones of the cranium in Dimetrodon are remarkably similar in position to those penetrating the same bones in Sphenodon. The condylar foramen transmitting the twelfth pair (hypoglossus) penetrates the exoccipital just anterior to the edge of foramen magnum. Its outer end opens in a notch (the incisura venæ jugularis Sieb.) in the side of the exoccipital. A little below and further forwards a second and much smaller foramen opens in the same notch; this may transmit either the ninth or tenth pair of nerves or a minor blood vessel. Passing forwards the notch deepens and is very soon converted into a foramen by the adjacent portion of the paroccipital. This is the foramen venæ jugularis of Siebenrock, and transmits the jugular vein and either the ninth or tenth nerves or both of them. In Sphenodon the foramen transmits not only these but the twelfth pair as well, the nerves being separated from the vein by very thin walls of bone, and may be separated from each other or have a common canal. The opening of the twelfth pair into the notch which forms the beginning of the jugular foramen is then very similar to the condition found in Sphenodon.

The fenestra ovalis, Fig. 6, F. O., is a single opening leading by a very short canal directly into the brain cavity, a character found in fishes and the amphibian Menopoma and existing imperfectly in some recent Reptilia, as the turtles. The same thing is described by Cope as existing in another Permian reptile, from the same horizon as the present specimen, but belonging to a separate family, the Diadectidae, and his order Cotylosauria. 69

The foramina for the seventh (facial) pair of nerves appear on the outer surface of the petrosal just anterior to the fenestra ovalis (Fig. 6, 7). They are located relatively a little further back than in *Sphenodon*. On the inner face of the same bone the foramina appear at the side of the base of the brain cavity a little anterior to their external opening. They are located just anterior to a slight ridge which defines the limits of the tympanic cavity. In *Sphenodon* this is about the point of location of a foramen common to the seventh and eighth nerves, which, however, almost immediately divides, the posterior branch penetrating the inner wall of the tympanic cavity and leading the auditory nerve to the inner ear.

The foramen for the fifth (trigeminus) nerve is completed from the incisura oto-A. P. S.—Vol. XX. F. sphenoidea by the membranous wall of the anterior portion of the brain case, as in Sphenodon and many lizards (Fig. 5, 6).

The deep pit excavating the lower surface of the basisphenoid is in all probability the lower opening of the Eustachian tubes. In most reptilian forms the tubes pass into

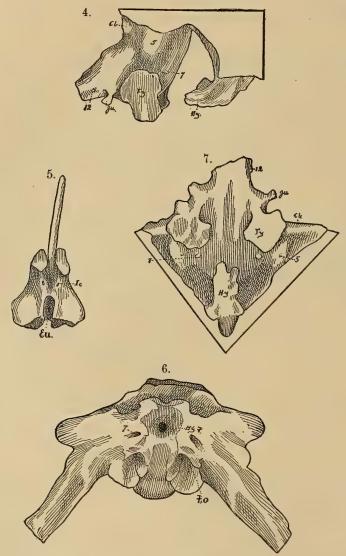


Fig. 4. Side view of a cast of the brain cavity.

Fig. 5. Lower view of the basisphenoid.

Fig. 6. Lower view of the cranial region.Fig. 7. Lower view of the cast of the brain cavity.

5. The trigeminus nerve. 7. The facial nerve. 12. The hypoglossus nerve. Ju. The jugular foramen. Ty. Cast of tympanic cavity. Hy. Hypophysis. Hy.F. Foramen penetrating base of basioccipital. F.O. Fenestra ovalis. I.C. Foramina for internal carotids. Eu. Opening of eustachian tubes. Cb. Cerebellum.

the pharynx in the neighborhood of the basioccipital-basisphenoid suture and anterior to the fenestra ovalis. In the Crocodilia and the aglossal batrachians they have a common

opening into the mouth. In the present form the tubes probably penetrated the large mass of cartilage covering the otic region and the posterior end of the basisphenoid and found a common opening in the deep pit described. It is difficult to imagine the use of such an extensive cavity in the basisphenoid, but in the *Teleosauria* an equally large cavity is found roofed over with bone. Anterior to this pit two foramina, Fig. 5, *I. C.*, penetrate the lower surface of the basisphenoid bone and on its upper surface a large foramen appears just posterior to the origin of the presphenoid rostrum. Through the pair on the lower surface the internal carotid arteries enter the bone and through the upper it gains access to the brain cavity by way of the pituatary fossa. On either side of the single foramen a pair of small foramina carry branches of the internal carotid. All of these foramina are very similar in position to the same ones in *Sphenodon*.

The cast of the brain cavity shows fairly well all parts posterior to the fifth pair of nerves, and the hypophysis anterior to them. As is well known, the brain in the Reptilia does not fill the brain cavity, but is supported by a mass of connective tissue carrying lymph and fat masses, so a cast of the brain cavity does not give an exact copy of the brain; however, many points can be brought out by such a cast.

If the cast be held with the short terminal portion of the medulla horizontal, the lower surface pitches downwards at a sharp angle to a point anterior to the tympanic region and then ascends as sharply to the point of origin of the hypophysis. The superior surface is horizontal and arched from side to side to a point over the tympanic cavity and there turns upwards at an angle of 45°. The angle thus produced is marked by a low, narrow ridge running across the cast and marking the position on the brain of a narrow and elevated cerebellum, Figs. 4 and 7, Cb., such as occurs in Sphenodon. This region was probably the seat of a large amount of connective tissue, and it is probable that the upper surface of the medulla descended at as sharp an angle as the lower. This would make still more marked the resemblance to Sphenodon and to the cast figured by Cope. This sharp bend of the medulla downwards is not found in other forms, though in the brain of Chelonia and some Lacertilia a bend is apparent.

The sides of the medulla show most posteriorly the beginning of the twelfth nerves, Figs. 4 and 7 (12), anterior to these the cast of the jugular foramen, Figs. 4 and 7, Ju., and finally the large casts of the tympanic cavity, Figs. 4 and 7, Ty. The nature of the matrix and the cavities prevented the tympanic cavities being cleaned so that the semicircular canals could be determined, but it is probable that they were very similar to those described by Cope.

Anterior to the tympanic casts a sharp constriction marks the ridge defining the limits of the tympanic cavity and then a sharp outswelling the point of exit of the trigeminus nerve, Figs. 4 and 7 (5). Near where these leave the body of the cast a small stub on each side marks the origin of the seventh pair, Figs. 4 and 7 (7).

The hypophysis is the most interesting feature of the brain. Descending between the anterior inferior process of the petrosal and turning posteriorly, it occupies a small notch in the posterior edge of the upper surface of the basisphenoid and then passes directly into the body of the basioccipital through the foramen mentioned. In the *Crocodilia* a somewhat similar condition exists. The basisphenoid is excavated for a considerable extent to accommodate the hypophysis. This makes it probable that the excavation of the bone is merely a secondary character to make room for the hypophysis, for in the *Crocodilia* the basisphenoid takes a large part in the floor of the brain-cast, and in the present form it is pushed so far downwards that it is excluded and the hypophysis encounters the basioccipital as soon as it turns toward the rear.

Marsh <sup>64, 65</sup> has described in the family *Atlantosauridæ* of his suborder *Sauro*poda of the *Dinosauria* a condition in which the pituatary cavity becomes a canal perforating the basisphenoid and opening into the pharyngeal cavity, considering it an embryonic character such as exists in the chick at the fifth day of incubation.

If the hypophysis occupied the entire cavity in the basioccipital it extended back nearly as far as the tympanic region and much further back than in most reptilian forms. In *Sphenodon*, the *Crocodilia* and some amphibians it reaches well back, but not so far as in the present form.

Compared with *Sphenodon*, the specimen shows the following points of resemblance. The foramina for the blood vessels and nerves are almost identical in position and nature. The contour of the medulla and cerebellum was similar and the hypophysis extended far back. The only point of difference is the excavation of the basioccipital to receive the distal end of the hypophysis. The free communication of the tympanic cavity is a character which is found in many existing primitive forms and is of secondary importance.

The points here brought out confirm the close relationship of *Pelycosauria* to the primitive *Rhyncocephalia* already asserted by Baur and Case.<sup>28</sup>

#### The Palate.

The following elements of the palatal region are preserved: both the pterygoids (the left nearly complete), the palatine of the left side, lacking the posterior portion and parts of the right one. No traces of the vomers have been found.

The pterygoids (Pl. I, Figs. 15, 16) are large bones which show three processes; an anterior horizontal one, becoming very thin in front and underlying the palatines; a posterior one, forming an extensive vertically expanded plate, and an external very massive ectopterygoid portion. The posterior plate leaves the massive part by a roundly trihedral neck; its lower edge runs downwards and backwards to the quadrate. The upper

edge is folded upon itself, forming a long and deep pit on the outer side. The edge is continued backwards horizontally, or even rising a little for nearly half the extent of the plate, and then falls off rapidly to join the inferior edge in a sharp point. The middle of this posterior edge is marked by a notch. It is possible that an anterior prolongation of the quadrate overlapped this part of the pterygoid, as it does in *Sphenodon*.

The massive part stands out from the plate-like portions; supported by a rather stout neck, it expands distally and its external face extended below the line of the teeth and formed an opposing process to the coronoid of the lower jaw. The upper end of the distal portion is injured on both sides, but probably bore a face for the ectopterygoid, which must have been present, as there is a distinct face for such a bone on the inner face of the jugal where it meets the maxillary. The ventral edge of the ectopterygoid process is rounded and bears eleven comparatively large teeth, which are placed in distinct alveoles and replaced from behind.

The anterior part is horizontal, the inner edge excepted, which is turned vertically upwards. The inner edges were close together and were united in the anterior part. The lower portion is covered nearly completely with small conical teeth—those on the outer and posterior region are the largest. A groove extends between this tooth-bearing region and a ridge marking the origin of the vertical plate. There are a few small teeth in the groove, and the ridge also bears a series of small teeth.

The pterygoids articulate with the basisphenoid processes just posterior to a point opposite the union of the ectopterygoid processes with the plate-like part. There are no faces on the pterygoid corresponding to those on the basisphenoid processes. The union must have been by ligament. The connection between the posterior processes with the quadrate was also ligamentous.

The palatines are strong bones, becoming more slender posteriorly. They are connected with the maxillary by their entire external edge by suture. The articular face is broadened and vertical. The inner portion of the ventral side of the palatines is covered with small conical teeth. The region bordering the posterior nares is preserved and determines their position, their posterior ends being just behind the large canine tooth.

The *vomers* are not preserved, but there are two small faces at the middle portions of the posterior line of the premaxillaries showing where they were attached. They were probably long and slender, paired and covered with small tubercular teeth. That the vomers were directly connected behind with the anterior processes of the pterygoids, excluding the palatines from the middle line, is very probable.

The *lower jaw* is represented by three bones—the *articular*, coössified with the *angular*, the *dentary* and a third bone, probably the *supra-angular*. The *dentary* contains twenty-seven teeth, which are located on a thickened ridge in alveoles. The first tooth is

slender and conical, slightly recurved. The succeeding two are nearly as large as the canine above; the remaining teeth are all small and recurved. The lower edge of the dentary is thin and marked internally with strong suture lines. The symphysis is short.

#### The Vertebral Column.

The vertebral column is represented by cervicals, dorsals and caudals.

The cervical vertebræ. The following cervicals are preserved: The atlas, with the exception of the neural arches, the axis, the third, the sixth, the seventh and the eighth. Two vertebræ, the fourth and fifth, are missing.

The atlas (Pl. II, Fig. 20). The centrum is broad above, antero-posteriorly, but below it is much contracted between the first and second intercentra. The anterior face is divided into an upper and lower part by a compression of the sides opposite the opening of the chordal canal. The lower part is saddle-shaped, and the upper somewhat convex. There are no traces of transverse processes. The posterior face is hidden by the second intercentrum and the axis, but another specimen shows a large opening of the chordal canal, in contrast to a very small one on the anterior face.

The first intercentrum, forming the lower piece of the atlas ring, is crescent shaped, with a broad lower rugose surface and a transverse concave keel above. The anterior face of the intercentrum is the largest, concave vertically and transversely, and lodges the lower part of the occipital condyle. The posterior face is convex from above downwards and occupies the saddle-shaped lower half of the anterior face of the atlas. The first intercentrum shows at the distal end below a facet on each side for the articulation of the single-headed atlas ribs.

The second intercentrum is similar to the first; the anterior and posterior faces are more equal. It is wedged in between the centra of the atlas and axis, and has the facets for the capitula of the axis ribs placed more to the middle of the posterior edge.

In the axis the centrum is well developed; on the ventral side a keel begins to appear. The posterior face of the neural spine is greatly expanded vertically at the base and greatly elevated. The posterior edge of the spine is thickened and divided by a groove which forms a deep cavity between the well-developed zygapophyses below. The apex is marked by a shallow triangular depression. The præzygapophyses are very small, with the articular faces directed downwards. The postzygapophyses are strong and elevated above the centrum. The articular faces look outwards and downwards and meet on the summit of a short keel below. The transverse processes project laterally and ventrally from the anterior part of base of the neural arch. The distal end does not become separated from the body of the neural arch, and is above the neuro-central suture.

The third cervical is badly injured by decay, but many points can be made out. The

articular faces are nearly round. The transverse processes curve outwards and downwards as in the axis, but the distal end reaches much further ventrally and is below the neurocentral suture for about a centimeter. The spine rises vertically from the centrum to a height of .147 m. It is broad and stout at the base, but suddenly contracts a short distance above it and ends in a slender rod curved slightly forwards. Between the bases of the præzygapophyses and the spine depressions exist, which become deep elongated pits in the dorsals.

Now follows a gap of two vertebræ. The sixth has a cylindrical body and round articular faces. The lower edges of the faces are extended ventrally, forming a slight flange or apron, which becomes very prominent in the posterior dorsals. The middle portion of the anterior edges on each side are reflected, forming an articular face. The transverse processes are short and stout, and stand out directly from the body of the neural arch. The articular face looks outwards and slightly backwards. From the anterior edge of the face a narrow process, bearing an articular face, runs down to the face on the anterior edge of the centrum. This shows that in the cervical region the capitulum and tuberculum of the ribs were still united.

The transverse process stands well above the centrum. There is a deep excavation at its base, running back to the notch between the posterior zygapophyses and the posterior edge of the centrum. This is interrupted near its middle by a ridge running up to the posterior edge of the transverse process. Superiorly the transverse process joins immediately the præzygapophyses, which are interrupted by a deep notch near their base. The articular faces of the postzygapophyses look outwards and downwards and meet on a small keel below. The faces of the præzygapophyses look inwards and upwards, and are slightly cupped.

The spine is thin at the base and somewhat elongate antero-posteriorly, with a thin, prominent ridge running up the anterior and posterior edges. A few centimeters above its origin the spine becomes rounded and then flattened antero-posteriorly. The ridges of the lower part disappear on the rounded part and are replaced by shallow grooves above. The spine has already reached a great height. The part preserved measures .385 m. in height, but this is only one-half of the spine.

The seventh and the eighth cervicals (Pl. II, Figs. 21, 22) differ only in degree from the sixth, the transverse processes become more slender and the face connecting the tubercular and the capitular faces nearly disappears. The pits above and below the transverse process become deeper and the body of the centrum is more compressed.

The first (?) dorsal is marked by a total disappearance of the capitular face on the anterior edge of the centrum. The centrum is a little higher and longer than broad. The ends of the chordal canal have broad funnel-like openings with flaring edges; the

canal becomes very small in the middle portion. The descending flange at the lower edge of the articular face has become much deeper than in the cervicals. The distal end of the transverse process has disappeared, but the base shows that it stood well out from the body of the neural arch. The slender process from the tubercular to the capitular face is still present, but incomplete at the proximal end, it still bears a small facet. The pit between the base of the transverse process and the base of the spine has become very long and deep, its anterior end is closed as abruptly as the posterior by the rising of the connection between the anterior end of the base of the transverse process and the præzygapophysis. The excavation below the transverse process is partly filled by a swelling out of the base of the neural spine and is contracted into a pit at a point posterior to the base of the neural spine. At the base of the præzygapophysis, the anterior edge of the centrum supports two small processes, one on each side of the neural canal. These correspond to similar processes on the posterior edge of the preceding centrum. The spine is nearly complete, its shape is the same as described in the cervical region, a plan which persists throughout the whole series of vertebræ. The spine is .872 m. long. or a little over twenty-five times the greatest diameter of the centrum.

The second dorsal differs from the first in a slight intensification of the characters.

The third and fourth dorsals are incomplete and injured by decay. A concavity of the sides of the centrum below the level of the chordal canal renders the keel quite thin and prominent.

The *fifth dorsal* shows a complete transverse process on the right side. The base presents a pinched appearance due to the presence of two deep pits, one above and the other below the base of the process. The anterior edge of the process has become broad and is marked by a deep groove. The tubercular face looks backwards and downwards, it is broad above and sharp below; from this sharp, lower, edge a narrow face runs down and inwards for a short distance, it is the remnant of the face connecting the tubercular and the capitular faces in the cervicals. The anterior and the posterior faces of the centrum are inclined slightly toward each other below and the vertical profile is slightly sigmoid, convex opposite the opening of the chordal canal and concave below it. This leaves quite a space between the lower edges of the opposing vertebræ to accommodate the intercentrum. The flanges descending from the lower edges of the articular faces have become quite broad vertically and the excavation of the lower half of the centrum is deepened so that the keel is thin and prominent. The edge of the keel is concave. The spine is incomplete, but even in its imperfect state over twenty-one times the greatest diameter of the centrum.

The sixth dorsal (Pl. II, Figs. 23, 24) shows a very slender base for the transverse

process; the pits above and below it are deep and the supporting ridges are slender. The process stands out nearly straight from the base of the spine.

The seventh dorsal closely resembles the sixth. The spine is practically complete; it is over twenty-four times the greatest diameter of the centrum with a length of .830 m.

The eighth dorsal shows a marked change in the transverse process which is directed forwards instead of straight outwards or backwards as in the anterior ones of the series. The distal end reaches in front of the anterior end of the centrum. The articular face for the tuberculum looks forwards and downwards, the face which formerly ran to join the capitulum has become a short process extending from one side of the tubercular face. The excavations of the side of the centrum have involved more than one-half of the vertical height, limiting the rounded part to the walls of the chordal canal. The descending flange of the articular face occupies fully one-third of their height and the edges have become very thin. The profile retains the sigmoid outline. To the anterior face of the centrum is attached the slightly displaced intercentrum. It is crescentic in outline and narrow from before backwards. The upper, concave part is divided into two nearly equal faces for the adjoining vertebræ. The lower surface is rugose and the upper posterior edges bear well-defined facets for the capitula of the ribs.

The ninth dorsal (Pl. III, Fig. 40) preserves both transverse processes entire. The connecting face between the capitular and the tubercular faces has entirely disappeared on the left side and is very small on the right. The upper edges of the anterior faces of the transverse processes have expanded forwards to join the prezygapophyses and roof over a deep pit below. The spine is nearly perfect. It ends in a slightly expanded rugosity. It is .863 m. long, or twenty-six times the greatest diameter of the centrum.

The tenth dorsal (Pl. II, Figs. 25, 26) has a more compressed body, the base of the transverse process is thin and expanded anteroposteriorly. The process curves forwards and reaches well in front of the anterior edge of the centrum. The posterior end of the centrum extends below the anterior end and causes the keel to slant toward the rear.

The eleventh dorsal has a very deep and narrow keel. The descending flanges on the faces of the centra take up nearly one-half of the vertical height. The posterior articular face extends below the anterior, giving the same oblique direction to the keel as in the preceding vertebra. An intercentrum belonging either at the posterior or the anterior end of the vertebra shows two well-developed faces for the ribs.

This is the last of the well-preserved dorsals. Posterior to the eleventh are five vertebræ that are badly injured by decay. In all of these the keel is very sharp and is inclined toward the rear. In the next to the last the anterior face is steeply inclined to the rear as it descends. The last two show round articular faces with only a very short

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descending flange. Two intercentra preserved are broad and less completely crescentic; they still show large faces for the capitula of the ribs.

There is no trace of vertebræ from the sacral region.

Five anterior caudals are preserved (Pl. II, Figs. 27, 28, 29). They have rounded articular faces with broad funnel-like openings of the chordal canal. The præ- and post-zygapophyses are somewhat elevated on the broad neural arches. The ribs are articulated to both the neural arch and the anterior edge of the centrum. The division is not complete into a capitulum and a tuberculum, but a deep groove on the posterior side of the proximal end nearly accomplishes this. They are doubtless free in the most anterior caudals. The ribs are short and slender. Those most anterior are the longest and leave the vertebra by a strong curve upwards. The distal end of each rib well below and in front of the anterior end of the centrum. The keels are low and rounded. The spines are incomplete, but were not, in all probability, so much elevated as in the dorsal series. The three most anterior of the preserved caudals are in the natural position and show that there was a considerable space between the lower edges of the centra. The spaces were filled by flattened intercentra with no facets for rib articulation; they were however attached ligamentously to the capitular head of the rib as this projected free from the edge of the centrum.

Several small vertebræ are preserved from the distal end of the caudal series. They are slender and cylindrical, biconcave and without spines or transverse processes. The gradual reduction of the series shows that the animal must have had a long and slender tail.

The scapula (Pl. III, Fig. 30) is falciform in outline. The body is elongate, expanded and quite thin distally. It is so bent upon itself near the proximal end that the main portion lay, in life, more nearly parallel to the vertebral column than perpendicular to it. The lower edge of this portion is concave upwards. The bone is very thin distally, but becomes thickened toward the middle of the shaft, due to the presence of a strong ridge running back from the posterior edge of the humeral face to lose itself on the distal end. A foramen penetrates the shaft just below the beginning of this ridge. The anterior and superior edges are injured by decay and are incomplete. Cope figures the anterior and the superior edges as nearly straight and as meeting at nearly a right angle. He also figures a face for the clavicle near the distal end. The scapula and the coracoid contribute about equally to the deep, obliquely placed cotylus for the humerus. The edges of this cavity are marked by two strong projections, the upper, belonging to the scapular portion of the region, looks forwards and downwards and the lower, the coracoid portion, looks backwards and upwards. The portion of the scapula bearing this face lies at almost a right angle to the rest of the bone.

The coracoid (Pl. III, Fig. 30) is small, quadrate in outline, with a thin anterior edge. The lower edge is thickened and deeply notched near its posterior angle. The portion anterior to the notch was considered by Cope as the procoracoid. The posterior edge is concave from behind forwards and becomes swollen in the region of the scapular articulation. The union of the scapula and the coracoid was accomplished only late in life and was probably never perfect.

#### Measurements.

	M.
Total length of scapula and coracoid	.276
Total length of coracoid	.067
Total breadth of coracoid	.058
Total breadth of distal end of scapula	.103
Greatest extent of humeral face	.069

The femur (Pl. III, Figs. 36, 37) is a strong and heavy bone, with well-developed articular surfaces. The proximal end is rounded posteriorly and deeply excavated anteriorly so that it is crescentic in section. There is no distinct head, the whole proximal end being rounded and thickened. There is a strong rugosity near the outer part of the convex posterior surface. The shaft is roundly quadrate in section. The distal end is divided by a deep groove into two strong rugosities, both bearing articular faces. The inner is the shorter and extends inwards at a small angle to the shaft. The articular face is almost entirely on the posterior surface and looks more backwards than downwards. The face is elongated vertically and notched on its inner edge by an extension of the popliteal space. The outer tuberosity is longer than the inner and is directed downwards. It bears two articular faces, one on the posterior surface, looking almost directly backwards, is nearly square in outline, the other is apparently for the head of the fibula; it is largely on the lower surface of the tuberosity and joins the posterior face by a narrow neck near its external side.

#### Measurements.

Total length	.220
Breadth of proximal end	
Breadth of distal end across condyles	.069
Greatest diameter of shaft at centre	.036

The humerus (Pl. III, Fig. 32) is without prominent condyles at the proximal end. The articular face is a wide, concave area lying across the laterally expanded proximal end at nearly a right angle. The inner angle of the proximal end is expanded into a prominent tuberosity. The outer angle is thin, flattened antero-posteriorly and continuous with the strongly developed deltoid ridge. The ridge stands at almost a right angle with the proximal end of the bone. It becomes very prominent with a rugose surface

and ends below by recurving sharply to the shaft. The lower end does not lose itself entirely on the shaft, but remains as a low ridge running down and inwardly to form part of the bridge over the entepicondylar foramen.

The distal end is expanded at nearly a right angle to the proximal end. The ulnar condyle is rounded, smaller than the radial, and somewhat diagonally placed on the outer extremity of the distal end. The face is unequally divided into two facets by a low ridge. There is no deep anconeal pit on the posterior face of the bone. The radial condyle, largely on the anterior face of the bone, is divided into a prominent, rounded external portion and an inner saddle-shaped portion. The inner portion bears no articular face, but is prominent and rugose. The entepicondylar foramen is situated near the upper part of this inner expansion and is enclosed by a strong bridge, the extension of the ridge upon the shaft of the bone. Above the ulnar condyle a deep notch represents the ectepicondylar foramen.

#### Measurements.

Total langth	M.
Total length	.181
Greatest breadth at distal end	.117
Greatest breadth at proximal end	.096
Diameter of shaft at centre	.024
Projection of deltoid ridge	.035

The ulna (Pl. III, Figs. 34, 35) is a slender bone, somewhat longer than the humerus, with a flattened shaft. The shaft becomes gradually smaller toward the distal end and then expands slightly again. The proximal end is excavated on its anterior face by a deep fossa looking, in the natural position of the bone, upwards as well as forwards. This cavity is divided by a low ridge into two facets, the larger looking forwards and the smaller and external one looking slightly outwards. This cavity is carried onto the upper face of the bone and divides the inner and outer portions of the proximal end. These extremities are produced above the articular face and form the olecranon process. The outer is the largest and curves inwards, presenting a convex, rugose surface. The distal end of the bone is divided into two distinct articular faces.

#### Measurements.

					М.
Total length			 	 	202
Greatest breadth a	t distal end		 	 	037
Greatest breadth a	t proximal	end	 	 	055

The radius (Pl. III, Fig. 33) is curved and shorter than the ulna. The shaft is lenticular in section with the edges becoming sharp and prominent toward the distal end. The proximal end is expanded and the articular face for the humerus is deeply concave

and somewhat crescentic in outline. The distal end is less expanded and the single articular face is a shallow pit, oblong in outline.

### Measurements.

	м.
Total length	.146
Greatest breadth proximal end	.042
Greatest breadth distal end	.038

The tibia (Pl. III, Figs. 38, 39) is greatly enlarged proximally. The shaft is slender and curved and the lower end is only moderately expanded. The cnemial crest is a strong ridge separated from the body of the bone by a deep fossa opening on the outer side. The fossa is continued onto the upper side of the bone as a deep pit which divides the articular face into two unequal halves, connected at their inner ends. These halves are again divided by a low trochlear ridge running fore and aft. On the posterior surface of the bone below the outer or fibular edge of the proximal end there is a strong, rounded swelling. The distal end is semicircular in outline, flattened before and rounded behind. There is no indication of a division of the distal end into articular facets.

#### Measurements.

	М.
Total length	.177
Breadth upper end from side to side	.072
Breadth upper end from before back	.051
Greatest diameter of shaft at centre	.021
Greatest breadth of distal end	.044

#### Conclusions.

The description here given of the genus *Dimetrodon*, together with the described characters of the forms mentioned in the historical review, enable a fairly complete characterization of the *Pelycosauria* to be given.

Teeth differentiated into incisors, canines and molars. Generally a diastema between the posterior incisor and the canines. The teeth without lateral cusps, but with the edges frequently serrated. The anterior incisors and the canines of the upper jaw much larger than the other teeth. The diastema in the upper jaw marked by a more or less deep pit at the point of union of the premaxillaries and the maxillaries. The alveolar edge of the upper jaw convex downwards and of the lower jaw concave upwards. The facial region greatly elevated by the expansion of the upper part of the maxillaries and the lachrymals. The region is quite narrow from side to side. The orbits large, round and located far back in the skull. The skull abruptly truncated posteriorly. The posterior aspect

of the skull, formed by a nearly vertical plate, concave from side to side, formed from the union of the exoccipitals, the supraoccipital, the basioccipital and the paroccipitals, the whole bearing a strong resemblance to the same region in *Dicynodon*. The upper and lower temporal arches both present; very short in the antero-posterior direction. The parietal and the superior arch descend rapidly to join the posterior end of the lower arch. The superior temporal vacuity much smaller than the lower. The quadrate greatly depressed and nearly enclosed by the surrounding bones. The lower face of the quadrate marked by two deep parallel grooves which received two corresponding processes on the articular bone of the lower jaw, thus limiting the motion of the lower jaw to the vertical plane. The nares open directly into the mouth at the anterior extremity. The pterygoids, palatines and vomers are covered by many small teeth. The ribs are two-headed in the dorsal region, the capitulum attaching to the intercentrum preceding. The neural spines of the vertebræ elevated or not. Limbs very short and strong. The humerus with an entepicondylar foramen and a notch representing the ectepicondylar foramen. The hind foot possessing both calcaneum and astragalus. A free centrale in the tarsus.

Under the *Pelycosauria*, as here defined, it seems possible to place with a considerable degree of certainty forms from all the regions which have furnished Permian vertebrate fossils. The following are the genera comprising the group as well as can be made out at present:

#### American forms:

Clepsydrops.

Dimetrodon.

Embolophorous.

Theropleura (doubtfully distinct).

Metarmosaurus (doubtfully distinct).
Archæobolus (doubtfully distinct).
Lysorophus.
Naosaurus.

#### Bohemian forms:

Naosaurus.

#### French forms:

Callibrachion. (?)

Stereorachis.

#### Russian forms:

Deuterosaurus.
Rhophalodon.

Cliorhizodon (?).

#### South African forms:

Ælurosaurus, Lycosaurus,

Cynodraco.
Cynosuchus (?).

South African forms:

Cynodontia.\*
Cynognathus.
Galesaurus.
Tigrisuchus.

Cynochampsa. Nythosaurus. Scaloposaurus.

There is little doubt that a considerable synonymy exists among the American forms. A majority of the genera were described from characters of the vertebræ alone and were founded on isolated vertebræ or on small series from separate regions of the spinal column. Thus Lysorhophus was founded on the fact that the neural arch is separate from the centrum, and that the capitular articulation of the rib is confined to the preceding intercentrum. In Theropleura the neural arch was free from the centrum and the capitulum of the rib was attached to the anterior end of the centrum. In Dimetrodon the "capitulum extended downwards and forwards to the anterior end of the centrum, but (as far as observed) there is no facet." In Embolophorous the capitulum of the rib is definitely described as joining the preceding intercentrum. As has been shown in the description of the skeleton of Dimetrodon, all of the conditions of the capitular articulation described in these genera are found in different parts of the column of the single specimen. The freedom or attachment of the neural arch within the group is hardly more than a character of age. Metarmosaurus was founded on the shortness of the centrum and the absence of the capitular face, exactly the conditions that are found in the posterior lumbar and the anterior caudals of *Dimetrodon*. There is little doubt that many of these genera are well founded, but only the consideration of a large amount of material will make it possible to clear up the synonymy.

The position of *Theropleura* is doubtful from the fact that the teeth are said to be the largest in the middle of the molar series, a character that is not common in the *Pelycosauria*, and is quite common in the American forms of the *Pareiasauria*. The same thing is true of the Russian form *Deuterosaurus*.

In our preliminary paper <sup>28</sup> the affinities of the *Pelycosauria* were discussed, as follows: "There cannot be any doubt that *Dimetrodon* is nearest to the *Rhynchocephalia* and *Proganosauria* (*Palæohatteriidæ*). The structure of the skull, the vertebral column, and the humerus are of the same type. The presence of a distinct squamosal and prosquamosal is of special interest. The same condition we find in *Sapheosaurus* H. v. Meyer (*Sauranodon* Jourdan) of the Jurassic *Sapheosauridæ*; and there is very little doubt that these two elements are also present in *Palæohatteria* Credner. The bone marked squa-

\*The group Cynodontia was considered by Seeley as worthy of separation from the remainder of the forms by the development of lateral tubercles on the teeth. To this character may be added the union of the superior and the inferior temporal arches, and the more or less complete obliteration of the superior temporal foramen. The Cynodontia are so close to the other forms of the group that it is impossible to separate them off even as a suborder, but they certainly do demand recognition for the advance in the development of the teeth and of the condition of the cranial arches toward the type of the Gomphodontia.

mosal by Credner is the prosquamosal; the true squamosal must have been free, and connected with the parietal processes.

"In Sphænodon the maxillary forms the lower boundary of the orbit; in Palæohatteria and Dimetrodon, the jugal excludes the maxillary from the orbit. The vertebræ with the well-developed intercentra, the ribs with the double articulations, can only be compared with those of the Rhynchocephalia and Proganosauria (Palæohatteriidæ). The presence of a free central bone in the tarsus of the Pelycosauria is an original character, which is shared only by the Palæohatteriidæ and Proterosauridæ; but in the Palæohatteriidæ tarsals 4 and 5 are free, in Proterosaurus and Dimetrodon they are united, to support metatarsal 4 and metatarsal 5. The humerus of Dimetrodon can be directly reduced to that of Sphænodon. The entepicondylar foramen is well developed in both; the ectepicondylar for amen of Sphænodon is represented by a very distinct ectepicondylar groove in Dimetrodon.

"The specialization of the *Pelycosauria* consists in the enormous development of the neural spines of the dorsal vertebræ, and in the reduction of the upper part of the quadrate and its nearly complete inclosure by the squamosal, prosquamosal and quadratojugal. It is quite evident, that the *Pelycosauria* with the two temporal arches and the specialized neural spines cannot be the ancestors of Mammals; they represent a specialized side branch of a line leading from the *Proganosauria* to the *Rhynchocephalia*, which becomes extinct in the Permian.

"The Mammals have a single temporal (zygomatic) arch; the posterior nares are placed far behind, and are roofed over by the maxillary and pterygoid plates; the quadrate is completely co-ossified with the squamosal and quadratojugal; the occipital condyle is double, the entepicondylar foramen is present in all the generalized forms. The ancestors of Mammals must show the same condition.

"Seeley <sup>45</sup> has combined a number of Permo-triassic *Reptilia* from South Africa into an order which he calls *Gomphodontia*. These Reptiles are: *Tritylodon* Owen (always so far considered a Mammal), *Diademodon* Seeley, *Gomphognathus* Seeley, *Microgomphodon* Seeley, and *Trirachodon* Seeley.

"In Gomphognathus we have a double occipital condyle; the posterior nares are placed far behind and are roofed over by the maxillary and pterygoid plates, and there is an entepicondylar foramen. The quadrate seems to be of the reduced form; a condition we see also in the closely related Cynognathus.

"These forms look very much like Mammals and could possibly be ancestral to them. We must suppose that the condition of the palate we see in the *Mammalia* and *Gomphodontia*, has been developed from a type we find among the *Rhynchocephalia*. The *Crocodilia*, where we have a similar palate as in Mammals, show us, how such a type

of palate was developed from the *Rhynchocephalia*, through the Belodonts and the Teleosaurs. It is possible, that the *Gomphodontia* originated from the *Proganosauria*. The question to be solved now is: What is the single temporal arch in the *Gomphodontia* and *Mammalia?* There are two possibilities; it represents either both the upper and lower arches united, or the lower one alone, the upper one being reduced.

"Seeley,<sup>67</sup> in his paper on the *Cynodontia*, gives a lateral view of the skull of *Cynog-nathus crateronotus*. There is a large supratemporal fossa, but besides, there is a small vacuity, between the squamosal and the jugal. If this vacuity is natural, it can only represent the infratemporal fossa. By the disappearance of this infratemporal fossa a single temporal bar would result. Further researches have to decide this very important question."

In a paper by the junior author <sup>66</sup> an attempt has been made to show that the vacuity here mentioned in the temporal region of *Cynognathus* is not a fracture, but the final stage in the final union of the two arches to form the zygoma of the mammals.

"A specimen of Cynognathus crateronotus, figured by Seeley, shows an opening between the upper and lower arches which was uncertain in origin, there being some reason to suppose it to be the result of an injury to the specimen, but a study of the figure of Procolophon, given by Seeley, shows the same condition. The enormous quadratojugal (called squamosal by Leydekker) joins the jugal in front, which in turn joins a slender element by its anterior superior corner; this element runs backwards, forming the lower and back portion of the orbit, and is undoubtedly the postorbital. Behind this element is another bone, the squamosal, or squamosal + prosquamosal, which rests upon the quadratojugal below; between all these elements is a small cavity, exactly as in Cynognathus. It is hardly probable that a break would occur in the same place in the two specimens, and so they are considered as showing the final stages of the union of the two arches to form the mammalian zygoma."

If these conclusions be correct there is an uninterrupted chain of forms from the most primitive of the *Pelycosauria* with two widely separated arches to the *Gomphodontia* with a single arch made up of the union of the two and in all probability to the Mammals also. With this progress in the development of the zygomatic arch goes a series of changes in other regions of the skull as the gradual assumption of the tuberculate forms of the teeth and the reduction of the quadrate bone.

The *Pelycosauria* now assumes a most important position in the mammalian-reptilian phylum. As stated in the paper last mentioned, <sup>66</sup> the group seems to be the beginning of the long line of forms that culminated in the Mammals.

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#### EXPLANATION OF THE PLATES.

# Plate I—Dimetrodon incisivus Cope.

#### All figures 1 natural size.

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Fig. 1. Premaxillary = pm.
Fig. 2. Nasal and maxillary = n, and m.
Fig. 3. Prefrontal = prf.
Fig. 4. Frontal = f.
Fig. 5. Parietal = p.
Fig. 6. Jugal = j.
Fig. 7. Postorbital = po.
                           Upper view, quadrate = q.; quadratojugal = qj.
Fig. 8.
            Suspensorial
Fig. 9.
                            Outer view, squamosal = sq.; prosquamosal = psq.
               region.
Fig. 10.
                           Lower view.
Fig. 11. Cranial region; upper view.
Fig. 12. Cranial region; lower view.
Fig. 13. Basisphenoid; lateral view.
Fig. 14. Basisphenoid; lower view.
Fig. 15. Pterygoid; external view.
Fig. 16. Pterygoid; lower view.
Fig. 17. Dentary = d.
Fig. 18. Articular region; articular = a.; angular portion of articular = an.
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## Plate II—Dimetrodon incisivus Cope.

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Fig. 19. First intercentrum.

a, lower; b, posterior view. \(\frac{1}{2}\).

Fig. 20. Centrum of atlas, second intercentrum and axis. \(\frac{1}{2}\).

Fig. 21. Seventh cervical; lateral view. \(\frac{1}{2}\).

Fig. 22. Seventh cervical; anterior view. \(\frac{1}{2}\).

Fig. 23. Sixth dorsal; anterior view. \(\frac{1}{2}\).

Fig. 24. Sixth dorsal; lateral view. \(\frac{1}{2}\).

Fig. 25. Tenth dorsal; lateral view. \(\frac{1}{2}\).

Fig. 26. Tenth dorsal; anterior view. \(\frac{1}{2}\).

Fig. 27. Three anterior caudals; lateral view. \(\frac{1}{2}\).

Fig. 28. An anterior caudal; anterior view. \(\frac{1}{2}\).

Fig. 29. The same; lower view. \(\frac{1}{2}\).
```

# Plate III—Dimetrodon incisivus Cope.

Fig. 30. Coracoid and scapula; left side. \(\frac{1}{2}\).

Fig. 31. Coracoid and scapula of Sphenodon; left side. 1.

Fig. 32. Humerus, left side; anterior view. \(\frac{1}{2}\).

Fig. 33. Radius, left side; anterior view. \(\frac{1}{2}\).

Fig. 34. Ulna, left side; anterior view. \(\frac{1}{2}\).

Fig. 35. Ulna, left side; lateral view. \(\frac{1}{2}\).

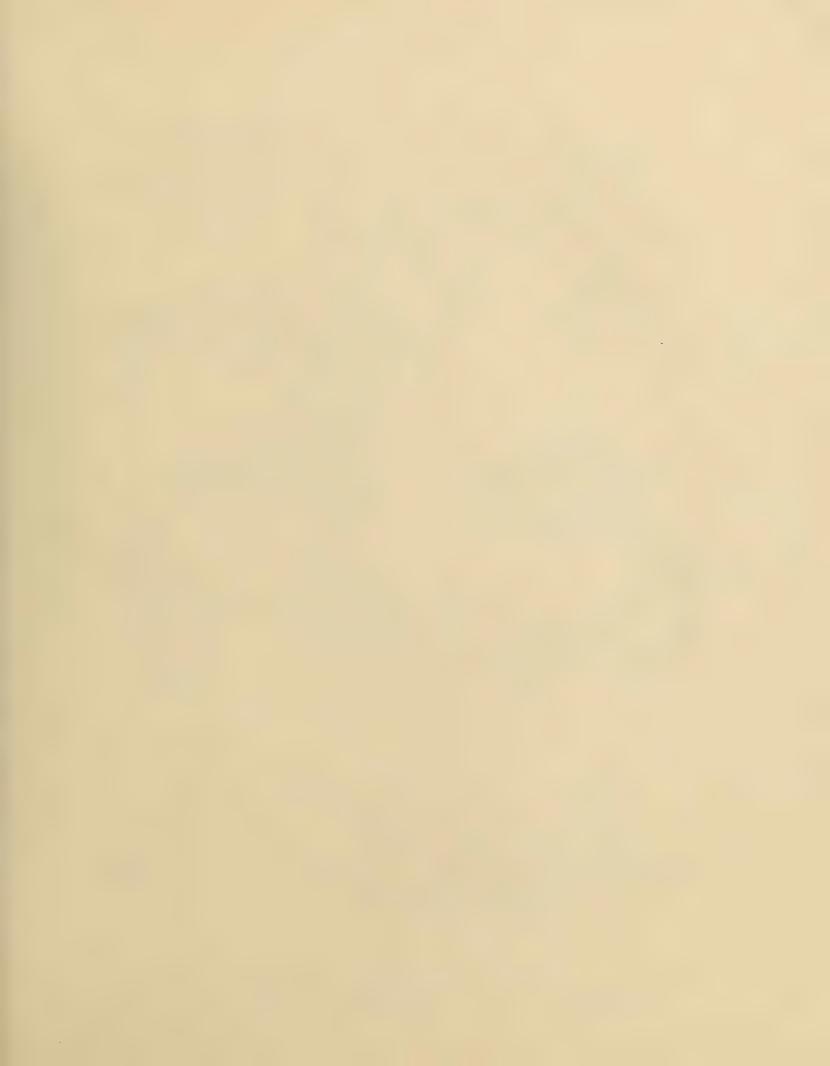
Fig. 36. Femur, right side; anterior view. \(\frac{1}{2}\).

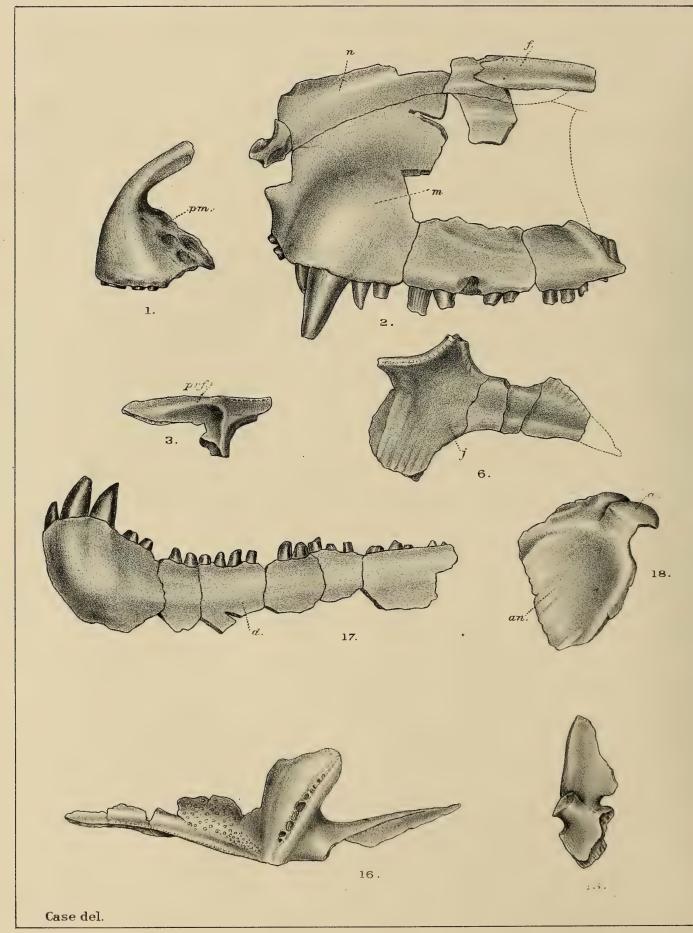
Fig. 37. Femur, right side; posterior view. \(\frac{1}{2}\).

Fig. 38. Tibia, right side; anterior view. \(\frac{1}{2}\).

Fig. 39. Tibia, right side; lateral view. \(\frac{1}{2}\).

Fig. 40. Ninth dorsal vertebra, complete; posterior view. \(\frac{1}{3}\).

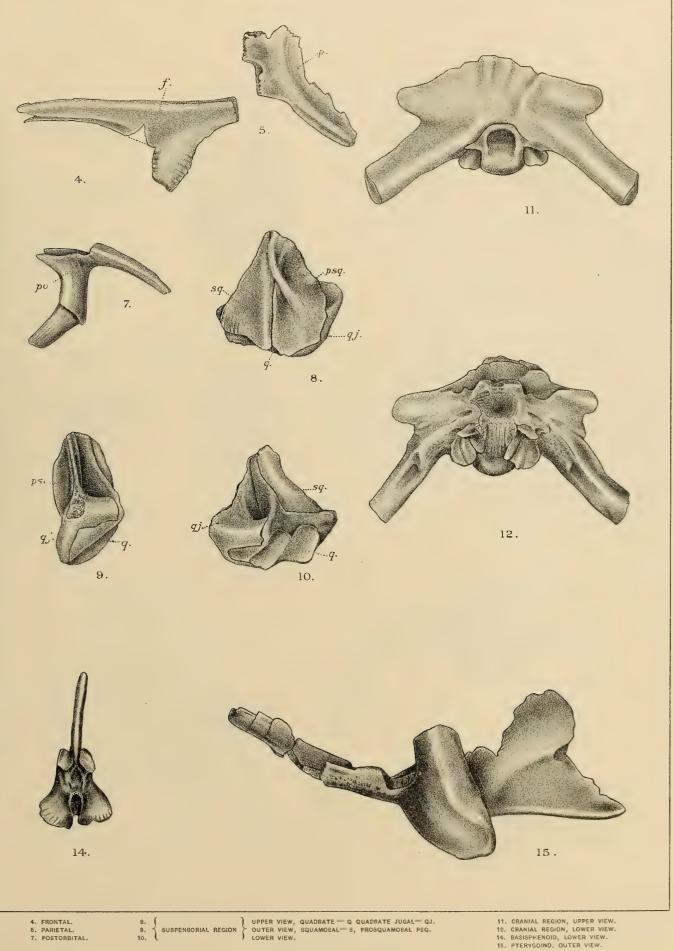




1. PREMAXILLARY. 2. NASAL AND MAXILLARY. 3. PREFRONTAL.

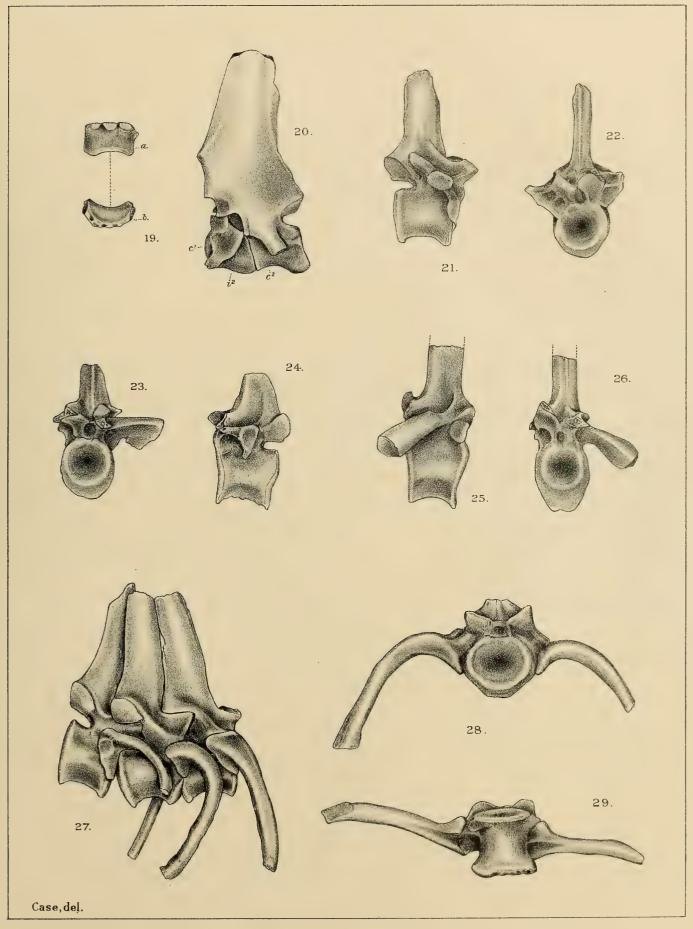
6. JUGAL. 13. BASESPHENOID LATERAL VIEW. 16. PTERYGOID, LOWER VIEW.

17. DENTARY. 18. ARTICULAR REGION, == A; ARTICULAR.



<sup>8.</sup> 8. 9. Suspensorial region  $\left. \right\}$  upper view, Quadrate == Q quadrate jugal= QJ. 0uter view, Squamosal= s, prosquamosal psq. Lower view.

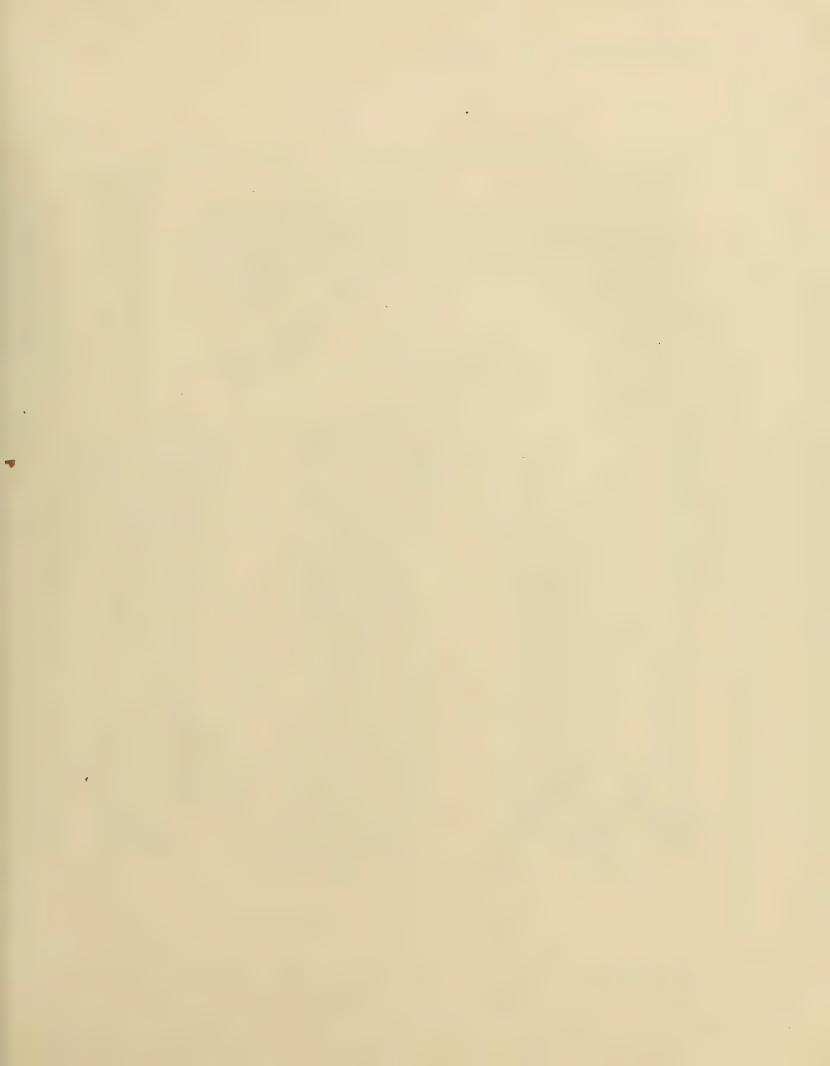


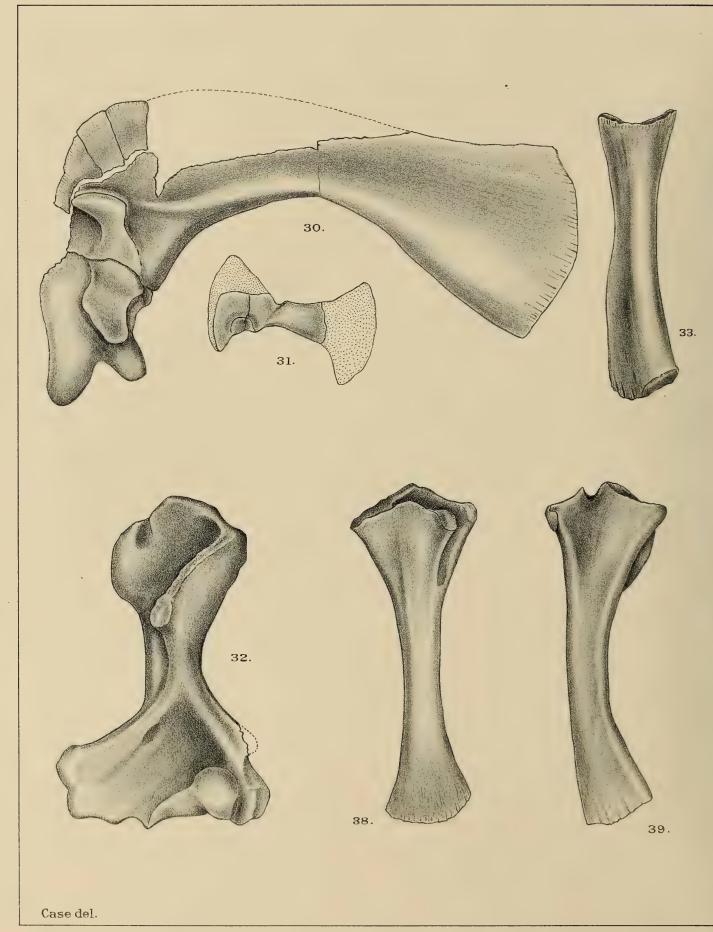


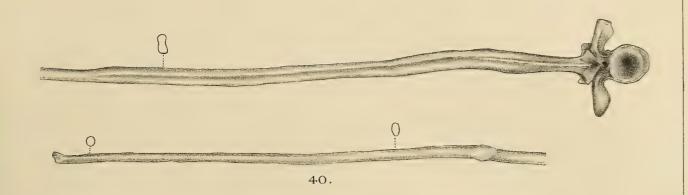
- 19. FIRST INTERCENTRUM.
  20. CENTRUM ATLAS, SECOND INTERCENTRUM AND AXIS.
  21. SEVENTH CERVICAL, LATERAL VIEW.
  22. SEVENTH CERVICAL, ANTERIOR VIEW.

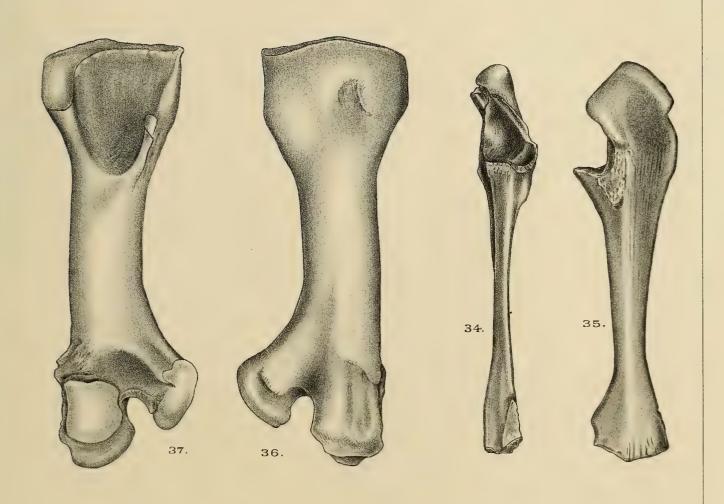
- 23. SIXTH DORSAL, ANTERIOR VIEW.
  24. SIXTH DORSAL, LATERAL VIEW.
  25. TENTH DORSAL, LATERAL VIEW.
  26. TENTH DORSAL, ANTERIOR VIEW.
- 27. THREE ANTERIOR CAUDALS.
  28. AN ANTERIOR CAUDAL, ANTERIOR VIEW.
  29. THE SAME, LOWER VIEW.

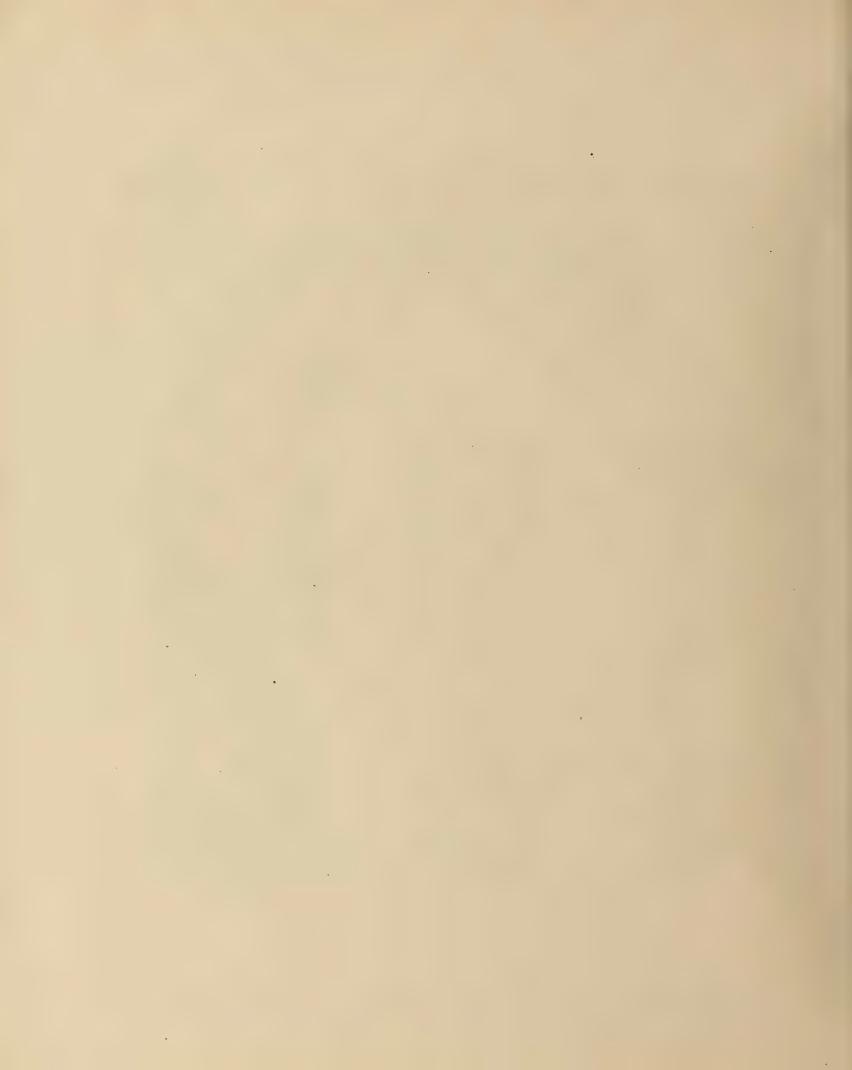














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